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A CHEMICAL AND MORPHOLOGICAL INVESTIGATION OF THE JACK PINE--LODGEPOLE PINE COMPLEX IN ALBERTA

by

© JOHN C. POLLACK

A THESIS

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled A CHEMICAL AND MORPHOLOGICAL INVESTIGATION OF THE JACK PINE--LODGEPOLE PINE COMPLEX IN ALBERTA submitted by JOHN C. POLLACK in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

ABSTRACT

The primary objective of this study was to determine which traits could be used to identify pure lodgepole pine (Pinus contorta var. latifolia) in a region where hybridization with jack pine (P. banksiana) commonly has been reported. Five xylem oleoresin monoterpenes of 592 individuals, and 17 morphological characters of 178 of the 592 individuals, in jack pine, lodgepole pine, and the putative hybrid stands in Alberta were measured. Of the 22 characters, α-pinene, β-phellandrene, and needle length best separated lodgepole pine from the combined group of jack pine and the putative hybrids. Of the five monoterpenes, α-pinene and β-phellandrene best separated the taxa. The oleoresin of morphologically pure jack pine at Cold Lake contained an average of 75.67% α-pinene, 10.76% β-pinene, 0.01% myrcene, 13.22% 3-carene, and 0.34% β-phellandrene. The oleoresin of morphologically pure lodgepole pine at Hinton contained an average of 7.96% α-pinene, 11.27% β-pinene, 2.62% myrcene, 20.79% 3-carene, and 57.36% β-phellandrene. The monoterpene composition of two putative hybrid stands at Onoway and Devon closely resembled the monoterpene composition of the Cold Lake jack pine stand, with the exception of a small group of suspected hybrid backcrosses to jack pine. The morphology of a tree did not always correspond to its monoterpene composition. Thus, the discrimination between lodgepole pine and the combined jack pine-putative hybrid group was accomplished best with the monoterpenes. Previously reported dominance in F_1 hybrids of jack pine pinenes made this

discrimination stronger than if the jack pine pinenes had been recessive.

Myrcene could be eliminated from the analyses since it was found to be a trace compound. Analysis of the other four monoterpenes in 14 stands allowed the identification of a transition zone between jack pine and lodgepole pine in the province. This zone occurred further to the west than reported by previous researchers. The transition zone immediately west of the two putative hybrid stands contained mixed stands of jack pine, lodgepole pine, and many hybrid monoterpene types.

The presence of variant monoterpene types in Front Range lodgepole pine stands from Coleman to Hinton, and the absence of such individuals in the Cypress Hills, provides evidence for the introgression of jack pine into lodgepole pine. No evidence of gene flow of lodgepole pine into jack pine was found in the Cold Lake jack pine stand. As the two putative hybrid stands are located on the eastern edge of the transition zone, these stands were interpreted as mostly jack pine, with a small complement of hybrid derivatives.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

I. INTRODUCTION

Natural hybrids between lodgepole pine (Pinus contorta Dougl. var. latifolia Engelm.) and jack pine (Pinus banksiana Lamb.) were reported in northern Alberta by A. C. Holman (Austin 1929). Later research showed that the range of the putative natural hybrids was extensive (Moss 1949, Lotan and Joye 1970, Scotter 1974), with numerous hybrid populations in central and northwestern Alberta. The scope of this study encompasses a detailed investigation of the nature of hybridization between these species in Alberta. Before discussing the direction and objectives of this investigation, the parental species will be introduced, and the previous research on the putative hybrids will be reviewed.

A. The Parental Species

Both lodgepole pine and jack pine belong to the hard pine group with its characteristic two- or three-needled fascicles, persistent fascicular sheaths, and generally armed umbos (Hosie 1973). The morphological characteristics of each species and the putative hybrids are given in Table 1.

Jack pine is a tree of the boreal forest, with a range extending from Nova Scotia to the central Northwest Territories, and from central Maine through Michigan to central Alberta (Figure 1). The species is typically short-lived. In the west, it occurs as wide-crowned, scrubby individuals in open stands on light, sandy acid soils. Occasionally jack pine occurs in dense stands as

straight, small-crowned individuals (Moss 1949). Common associated species include trembling aspen (Populus tremuloides Michx.) and paper or white birch (Betula papyrifera Marsh.). There is little interspecific competition in most stands (Fowells 1965, Hosie 1973).

Lodgepole pine is a western species ranging from Baja, Mexico to southeastern Alaska, and east to central Alberta and the Black Hills of South Dakota (Figure 1). Within its range at least four distinct races are recognized (Critchfield 1957). The Mendocino-White Plains race (ssp. bolanderi) is a dwarfed, inland Californian race with serotinous cones and short, wide needles. The Sierra-Cascade race (ssp. murrayana) is a large diameter, thin-barked race with nonserotinous, nonpersistent cones and wide, short needles. The Coastal race, shore pine (ssp. contorta) consists of small, short-needled, thin-barked individuals with low cone serotiny which increases as one moves inland. The Rocky Mountain-Intermountain race (ssp. latifolia) consists of tall, small diameter individuals with predominantly serotinous cones and long needles. Semi-erect and erect cones are present only in this race of lodgepole pine (Critchfield 1978).

It is this latter race of lodgepole pine, Pinus contorta var. latifolia, which is involved in the putative hybridization with P. banksiana in central Alberta and the Northwest Territories (Figure 2).

In Alberta, lodgepole pine typically occurs as tall, narrow-crowned individuals in dense stands on heavier soils. Associated species include trembling aspen and white spruce (Picea glauca

(Moench) Voss.) on drier sites, and black spruce (Picea mariana (Mill.) B.S.P.) on wet sites. Both lodgepole and jack pine occur together on some sites, such as the sand hills southwest of Grande Prairie, Alberta (Moss 1949).

B. Previous Research on the Putative Hybrids

The first report of putative natural hybrids between Pinus contorta var. latifolia and Pinus banksiana was made by A. C. Holman (Austin 1929) after observations in northern Alberta. Moss (1949) examined 32 pine stands in the province; he noted a large number of the putative hybrids in the region between Peace River, Lesser Slave Lake, and Pigeon Lake. These trees were morphologically intermediate to the parental species; some individuals had 50% aborted pollen. Putative hybrids were most abundant in those areas where the two parental species' ranges overlapped, and in those stands which contained both parental species. Beyond the area of overlapping ranges, or in those stands containing only one of the parental species, the putative hybrids were rare. Isolated putative hybrids as far east as Riding Mountain, Manitoba, led Moss to suspect that introgression of lodgepole pine into jack pine had occurred.

Mirov (1956) examined a swarm of the putative hybrids near Heatherdown, Alberta. The steam volatile fraction of the xylem oleoresin was evaluated using index of refraction and specific density. Lodgepole pine from sources beyond the suspected hybridization zone contained primarily β-phellandrene, whereas similarly isolated jack pine contained primarily pinenes. The hybrid pines

contained a mixture of the monoterpenes. Of considerable interest within the hybrid swarm were certain morphologically pure lodgepole pine trees which were chemically identical to jack pine.

It is worthwhile to review the importance of the monoterpenes in chemotaxonomic studies. A family of secondary metabolic compounds with a general formula of $C_{10}H_{16}$ monoterpenes are a diverse group of acyclic, monocyclic, and bicyclic derivatives of an acetate-mevalonic acid pathway (Geissman and Crout 1969). Hanover (1966) found that the monoterpene composition of western white pine (Pinus monticola Dougl.) was not significantly influenced by environment. A number of ramets possessed identical monoterpene compositions after establishment on three different sites in Idaho. In addition, slight but consistent variation was noted in monoterpene composition of tissue of different ages, and in tissues from different aspects of the tree. By far the greatest source of variation in monoterpene composition occurred as among-tree variation. Smith (1977) found similar results in ponderosa pine (Pinus ponderosa Laws.).

Zavarin et al. (1969) examined the inheritance of xylem oleoresin monoterpenes of seven pure jack pine trees, 17 pure lodgepole pine trees, 32 F_1's, six F_2's, 41 F_3's, 18 backcrosses to jack pine, and nine putative natural hybrids. The compound which best separated the controlled crosses from the parental species was β-phellandrene. The hybrids contained 3.2-8.5% β-phellandrene, while jack pine only contained trace amounts, and lodgepole pine contained 10.0-27.0%. The amount of 3-carene in the hybrids usually was similar to the trace amounts present in jack pine, yet a few

trees had amounts equal to the higher lodgepole pine concentrations. The backcrosses to jack pine resembled jack pine chemically, with the exception of one tree with 3.2% β-phellandrene. Five of the six F_2's chemically resembled the F_1 generation. The backcrosses of the F_2's to jack pine were identical to jack pine except for the 3-carene concentration, for which half of the trees had more than trace amounts. Most F_3 trees were similar to the F_1 hybrids.

The authors speculated that the many indications of segregation in the data implied that monoterpene composition in the hybrids was controlled by relatively few genes. It was, however, impossible to validate an inheritance pattern since neither F_2 nor F_3 progeny attained parental lodgepole pine concentrations of β-phellandrene.

Lotan and Joye (1970) reported evidence of introgression of jack pine into lodgepole pine near Bozeman, Montana, which is far removed from the present zone of overlapping ranges. The monoterpene compositions of two of the eleven lodgepole pines examined resembled jack pine.

Pauly and von Rudloff (1971) found a more complex monoterpene composition in the leaf oil of lodgepole pine than in the xylem or cortical oleoresin. The major compounds in the steam volatile fraction of the leaf oil were β-phellandrene (34%) and β-pinene (30%). They noted that the intra-tree variation in leaf monoterpenes at different heights was small, while the inter-tree variation was large. Populations at Bragg Creek, Kananaskis, and Eisenhower Junction, Alberta, had similar monoterpene compositions, while those at Jasper, Hinton, and Edson contained some individuals with

monoterpene compositions resembling jack pine. While concluding that their sample size was too small to give reliable values for Alberta lodgepole pine populations, they suspected that the trees which chemically resembled jack pine were evidence of introgression of jack pine into lodgepole pine. Certain trees in jack pine stands in Saskatchewan and Ontario were found by von Rudloff (1975) to resemble lodgepole pine in monoterpene composition. He concluded that such widespread introgression would be unlikely in the interval since the two species' ranges overlapped at the end of the Wisconsin glaciation. This conclusion conflicted with the previous theory on introgression advanced by Pauly and von Rudloff (1971).

Scotter (1974) identified putative hybrids at 13 localities in the South Nahanni River and Flat River region of the Northwest Territories. This apparent range extension had been first noted by Critchfield and Little (1966) in a distribution map for jack pine and lodgepole pine.

Hellum (1966) assessed the degree of species purity at 18 localities in Alberta and the Northwest Territories using a hybrid index based on 10 morphological traits. He concluded that each pine species exhibited varying purity far from the hybrid area.

C. Study Objectives

Interest in the accurate identification of natural hybrids between lodgepole and jack pine has increased with the initiation of a lodgepole pine improvement program by the Alberta Forest Service. It is well known that interspecific hybridization can

produce progeny possessing highly variable and sometimes deleterious traits (Stebbins 1958). Progeny of controlled crosses between lodgepole and jack pine exhibit increased susceptibility to eastern gall rust (Cronartium quercuum Berk.) and sweetfern rust (Cronartium comptoniae Arth.) compared to local jack pine sources in Minnesota, Wisconsin, and Michigan (Anderson and Anderson 1965). As the vigor and disease resistance of the various hybrid derivatives remain unknown, the mistaken inclusion of hybrid pines into a lodgepole pine breeding scheme could produce difficulties later in the program.

Mirov (1956) noted that the putative hybrid swarms contained a heterogeneous mixture of individuals, some of which morphologically resembled lodgepole pine, yet chemically resembled jack pine. The natural hybrid swarms conceivably contained a complex mixture of the two parental species and various hybrid derivatives. In areas where hybridization is common, it will be difficult if not impossible to choose relatively pure lodgepole pine for tree improvement programs unless one can determine first the structure of the hybrid populations, and then those characters which best separate lodgepole pine from the hybrid pines.

The purpose of this study was to examine the morphological and chemical characteristics of members of the putative hybrid swarms, elucidate the composition of those swarms, and determine how one could identify individuals from those swarms. The specific objectives are:

1. To describe the population structure of these natural hybrid populations based on the morphological and chemical

characteristics of individual trees.

2. To determine if simple quantitative or qualitative characters can be used for the separation of lodgepole pine from jack pine and the various hybrid derivatives in Alberta.
3. If possible, to map the distribution of the putative hybrids in Alberta.

D. Limitations to the Study

In taxonomic studies, the measurement of phenotypic characters is actually the measurement of the sum of genetic, environmental, and interactive factors which contribute to the observed characters. This relationship can be expressed in the equation:

$$P = G + E + I$$

where P = phenotypic expression of a character

G = genetic influence

E = environmental influence

I = interaction between genetic and environmental factors

In natural stands, the environmental component of the observed phenotypic variation is unknown. This unknown component complicates phenotypic comparison among stands, as one cannot assume that this source of variation will be equal in all natural stands. A common solution to this problem is to use progeny from natural stands in common garden or greenhouse experiments. Under controlled conditions, the environmental variation will be measurable; thus, it can be eliminated in subsequent comparisons.

Unfortunately there are a number of factors which complicated the use of a controlled experiment in this case, and suggested *ex post facto* research in mature, natural stands. One factor was the long generation times of the species, which reduced the attractiveness of controlled crosses and subsequent planting of progeny under controlled conditions. Also, the putative hybrid swarms were expected to contain a complex mixture of crosses and backcrosses which may not be duplicated in one or two generations of controlled crosses. Finally, mass selections for an improvement program would be made in natural stands. Any method for discriminating lodgepole pine from jack pine and the putative hybrids must be applicable to the natural stands.

Thus, it was decided to examine natural stands despite the larger, unequal, and unknown components of environmental variation which would be retained in the results. This methodology will not overly influence the monoterpene characters, since the strong influence of genetic versus environmental factors on monoterpene composition has been demonstrated in a number of heritability studies (Hanover 1966, Squillace 1976, Smith 1977).

E. Hypotheses

The study was conducted in two stages. The first stage--the population study--examined four natural pine stands. Two of the stands are easily accessible putative hybrid swarms near the Heatherdown, Alberta site studied by Moss (1949) and Mirov (1956). Morphologically pure lodgepole pine and jack pine stands were chosen

at Hinton and Cold Lake, respectively, to serve as controls for the measurement of parental characteristics. The population structure (i.e. the presence of any groups with distinct chemical and morphological characters) of the hybrid stands could be examined using factor and cluster analysis. Similar analyses of the "pure" stands would provide a basis of identifying the hybrid stand individuals and groups as either hybrid or typical of one of the parental species. In addition, those variables which best separated lodgepole pine from jack pine and the putative hybrids were determined by principal component, cluster, and discriminant analysis. Partial validation of hybrid classifications was possible through the chemotaxonomic work with controlled jack pine and lodgepole pine crosses by Zavarin et al. (1969).

The population study dealt solely with these four stands to fulfill the first two objectives, which are framed as Hypotheses 1 and 2:

Hypothesis 1: There are no intra- or inter-population structures, as defined by the measured characters, in the population study stands.

Variables: As listed in Table 2.

Analysis: Principal component and cluster analyses.

Hypothesis 2: There are no variables (characters) which can separate morphologically pure lodgepole pine from jack pine and the putative hybrids.

Variables: As listed in Table 2.

Analysis: Discriminant analysis.

The second stage of the study--the monoterpene survey--examined the monoterpene composition of individuals in 14 stands throughout Alberta to meet the third objective. A discriminant function based on the results of the population study was used to classify individual trees, according to their monoterpene composition, as either lodgepole or jack pine. These classifications, combined with provincial concentration maps for the four major monoterpenes, were used to determine the species composition of pine stands in Alberta.

II. METHODS AND MATERIALS

A. Site Description

The 14 study stands were relatively disease-free and at least 40 years of age (Figure 2 and Table 3). The four intensively sampled stands used in the population study were a subset of the 14 stands used in the monoterpene survey.

B. Sample Collection and Storage

Eighty relatively disease-free and unwounded individuals were selected in each of the four stands used in the population study. Sample size per population was based on work by Smith (1977) and by calculating sample sizes using data from Pauly and von Rudloff (1971). Xylem oleoresin samples were collected from each tree between August 25 and September 7, 1978. A 40 mm by 2 mm hole was drilled at 1.5 m height on the south side of the bole of each tree. A 50 µl disposable micropipet was inserted in the hole. When full, the pipet was removed, broken into a 1 dram screwcap vial, and kept at 0 degrees C. until brought to the laboratory. In the laboratory the samples were diluted to 1.8 ml with chloroform and refrigerated at -12 degrees C. until gas chromatographic analysis.

Pollen was collected from each tree in late May 1978. Two seed cones were collected from each of three mid-crown branches on the south side of each tree. Two three-year needles from different fascicles were collected from each of four mid-crown branches on the

south side of each tree. Needle and cone sample sizes were based on work by Critchfield (1957).

Pollen samples were stored at 0 degrees C. over calcium chloride in dessicators, while needle samples were frozen until the time of analysis.

The ten additional stands used in the monoterpene survey were sampled only for xylem oleoresin. Forty trees per stand were tapped. Collected samples varied from 25 to 39 individuals, according to the air temperature on the collection day. Sampling and storage techniques were identical to those used in the intensively studied stands.

C. Laboratory Analysis

Five monoterpenes in the oleoresin were identified with gas chromatography (g.c.) using standards, relative retention times, and peak enhancement methods (Szepesy 1970). Two columns--3% SE-30 and 5% Carbowax 20M--were used for the monoterpene identification. In addition, a g.c.-mass spectrometric analysis was performed to verify the g.c. identification.

Quantitative analysis of the samples was performed on a 3% SE-30 column with a 5830A Hewlett Packard gas chromatograph (Table 4). An external standard was run after every ten sample runs during analysis. Normalized monoterpene percentages were calculated using the equation:

$$NP_i = \frac{A_i \cdot r_i}{\sum_{i=1}^{n} A_i \cdot r_i} \times 100$$

where NP_i = normalized percentage of the ith compound

A_i = area under the ith peak

r_i = detector response correction factor

n = number of compound peaks

One hundred pollen grains from each tree were examined to determine physical abortion percentages. A grain was considered to be aborted if it was shrunken or misshapen to less than 75% of the average diameter of other normal grains in the sample. Three needle and 12 cone characters were based on the average measurements of eight needles and six cones (Table 2 and Figure 3).

D. Univariate Analysis

A number of univariate statistics were calculated for comparative purposes, and to prepare the isoconcentration maps. The SPSS subprogram CONDESCRIPTIVE (Nie et al. 1975) was used to calculate the mean, minimum, maximum, standard deviation, standard error, skewness, and kurtosis of the 22 variables in the four stands of the population study. Only means were calculated for the 14 stands of the monoterpene survey.

The subprogram NONPAR was used to perform Kolomogov-Smirnoff test for normal distribution (Nie et al. 1975, Gibbons 1976, Precht 1977) on all variables in each stand of the population study ($\alpha = .05$). The Kruskal-Wallis analysis of variance (Nie et al. 1975, Gibbons 1976, Precht 1977) was used to test for significant differences among the means of the 22 variables in the four stands of the population study.

E. Multivariate Analysis

In the population study, the tests of the first and second hypotheses were performed with a variety of multivariate analyses. The order of, and results obtained from, these analyses are summarized in Table 5. The first multivariate procedure involved principal component analysis of the four data sets. The first data set consisted of 22 morphological and monoterpene variables per individual for all four stands. The second data set involved only 5 monoterpene variables per individual for the four stands. The third data set consisted of 22 variables per individual for the two putative hybrid stands. The fourth data set contained only 5 variables per individual for the two putative hybrid stands.

Principal component analysis is a technique which reduces the original variables in a data set to a smaller number of artificial variables or principal components (Green 1978). Each principal component is a linear equation containing all variables from the original data set. The first principal component axis accounts for the maximum amount of variation in the original data set which can be expressed in a single linear equation. The second principal component axis is orthogonal to the first axis; it contains the maximum possible amount of the remaining variation. Subsequent principal component axes likewise are orthogonal and account for a maximum of the remaining variation during their derivation.

When performing a principal component analysis, one can reduce the dimensionality of the original data while preserving most

of the original variation. This is useful with highly dimensional data if the first two principal component axes contain a large percentage of the total variation in the original data. Often a plot of the data on the first two axes can provide a simple yet accurate representation of the distribution of individuals and groups. Also, principal component scores can be generated for subsequent cluster analyses. The major advantage of using principal component scores in cluster analysis is their orthogonality, since strongly correlated variables can produce erroneous clusters.

Principal component analysis was performed using the SPSS subprogram FACTOR and the PA1 method without rotation of the principal component axes (Nie et al. 1975). An eigenvalue cutoff criterion of 1.00 was used to determine the appropriate number of principal components to be retained (Kaiser 1959 in Green 1978). Plots were made of individuals' scores on the first two principal component axes for all four analyses.

The principal component scores generated by the four principal component analyses were used in subsequent hierarchical cluster analyses. In cluster analysis, one examines the relative positions of individuals, each described by n variables, in an n-dimensional hyperspace (Sneath and Sokal 1973). The objective of this cluster analysis is to identify natural associations or clusters of individuals within the hyperspace. A hierarchical clustering method starts with an initial number of clusters or operational taxonomic units (OTU's) equal to the number of individuals (q) in the data set. Using a similarity criterion, the two most similar OTU's are fused

into q-1 clusters. The similarity matrix is recalculated after each fusion, and the next most similar OTU's are fused. The process is continued until only one cluster remains.

Cluster analysis was performed on the principal component scores from each data group using the hierarchical Ward's and relocate methods (Sneath and Sokal 1973, Wishart 1978) from the Clustan 1C package (Wishart 1978). These clustering methods find minimum variance clusters using within-groups error sum of squares similarity coefficients. The procedure was to use the principal component scores for each individual to load the cluster analyses. As is common with medium-sized populations (Wishart 1978) a Ward's cluster analysis was performed to reach a suboptimal solution. The Ward's classification was then used as a starting point for a relocate cluster analysis. A second relocate run using a random, ten-cluster start was performed last of all. The results of the three runs were compared to determine if a global optimum existed. The similarity coefficients from the first relocate run were graphed to determine the proper number of clusters. In all cases, the selection of an appropriate number of clusters was made at the point where the curve became exponential.

The final step in the population study used the clustering results in discriminant analyses. Discriminant analysis derives a set of discriminant functions to distinguish among groups or OTU's (Green 1978). Each discriminant function is a linear equation which contains some or all of the original variables. The function has maximal variance between groups relative to the within group variance.

During discriminant analysis, univariate F ratios for all variables were calculated to determine which, if any, variables showed significant differences among groups. These tests were used to evaluate the first hypothesis for each cluster analysis. However, as Green (1978) cautions, any test for significance after clustering is suspect, as sampling is no longer random. The choice of a univariate F test for all variables, then, was primarily to locate significant differences in variable means among groups.

Once discriminant functions were calculated, the strength of the original clusterings could be tested by using the functions to classify the same individuals used to derive the functions. If a large percentage of these individuals were correctly classified, then the original clusters were distinct, and the derived discriminant functions are a powerful means of classification.

In the population study, discriminant analysis was used to determine the strength of the separation of clusters located during cluster analysis, and to determine which characteristics best separated these clusters. Four stepwise discriminant analyses using Rao's criterion (Nie et al. 1977) for variable inclusion were performed on the results of the cluster analyses. The results of the discriminant analyses test the second hypothesis.

The monoterpene survey involved a stepwise discriminant analysis using Rao's criteria and the four major monoterpenes of trees in the Hinton and Cold Lake stands. Once a discriminant function was derived, the monoterpene data for individuals from all 14 stands were subjected to classification as either lodgepole pine or

jack pine. The classification, along with the isoconcentration maps for the four major monoterpenes, fulfills the third objective. A plot of the discriminant scores of the Hinton and Cold Lake stands and two highly mixed (by discriminant classification) monoterpene survey stands was made to identify suspected hybrids in these stands.

III. ANALYSIS AND RESULTS

A. Univariate Analysis

The Population Study

The means of the 22 variables for each of the four stands are given in Table 6. Kolmogorov-Smirnov tests (α=.05) on the 22 variables in each of the four populations indicated that 12, 11, 11, and 11 variables in the Hinton, Onoway, Devon, and Cold Lake stands, respectively, did not possess normal distributions (Tables 7 to 10). It was noted that the strongly bimodal distributions in some variables, particularly α-pinene and β-phellandrene, were responsible for the rejection of a normal distribution hypothesis.

These results indicate that the application of such parametric techniques as Duncan's multiple range or Scheffe's tests would be inappropriate for many of the variables. Accordingly, Kruskal-Wallis analysis of variance was used to test for significant differences between populations. Two sets of analyses of variance were made (Tables 11 and 12). The first compared the Hinton population with the remaining three stands; the second compared the Cold Lake stand with the remaining three stands. It can be seen that 18, 16, and 21 of the variable means in the Hinton stand are significantly different (α=.05) from the Onoway, Devon, and Cold Lake stands, respectively. Only 12, 13, and 21 variable means in the Cold Lake stand were significantly different (α=.05) from the Onoway, Devon, and Hinton stands, respectively. These tests demonstrate that the putative hybrid stands differ from the jack pine stand in 56.8%

of the measured variables, while the putative hybrid stands differ from the lodgepole pine stand in 77.3% of the variables. Thus, the putative hybrid stands resemble the jack pine stand more closely than the lodgepole pine stand.

The Monoterpene Survey

The means for the five monoterpenes in the 14 stands of the monoterpene survey (Table 13) were used to construct isoconcentration maps for α-pinene, β-pinene, myrcene, and β-phellandrene (Figures 4 to 7). It is apparent that the concentrations of these major monoterpenes are not random in the province, but follow distinct trends. Owing to the sparse occurrence of pine stands north of Grande Prairie, the isoconcentration line locations may be misleading, in that they suggest a continuous distribution of pine stands in northern Alberta.

B. Multivariate Analysis

The Population Study

Tests of the hypotheses. In the four multivariate analysis sequences which follow, it is apparent from the univariate F tests that highly significant differences existed among the groups derived from cluster analysis. Accordingly, Hypothesis 1 was rejected. Distinct population structures or groups exist in all analyses.

Discriminant analyses on the groups obtained from the cluster analyses involving all four stands showed that subsets of the original variables could be used to separate nearly all of the lodgepole pines from members of the jack pine and putative hybrid stands. In addition,

the five monoterpene variables were found to be nearly equal to the full 22 variables in discriminatory power. Thus, Hypothesis 2 must be rejected. Specific characters exist which can be used to separate morphologically pure lodgepole pine from jack pine.

All stands--22 variables. Principal component analysis of the 22 variables for all stands yielded seven principal component axes or factors which accounted for 81.0% of the total variation in the original data (Table 14). The first two factors accounted for 34.0% and 16.1% of the original variation. Factor loading was complex. The first axis loaded heavily (e.g. possessed large factor score coefficients) on β-phellandrene, α-pinene, spine length, and needle length, while the second axis loaded heavily on bulge length, bulge length/cone length ratio, and bulge length/cone width ratio. A plot of the first two factor axes clearly showed a wide separation between members of the lodgepole pine stand and the other stands (Figure 8). Based upon the 22 characters, the putative hybrid stands were more closely associated with the jack pine stand than the lodgepole pine stand.

A graph of the similarity coefficients from the first relocate group analysis suggested a five cluster solution (Figure 9). The five groups from this solution were plotted on the first two factor axes (Figure 10). Membership percentages of the groups showed substantial mixing of the original stands, with the exception of the Hinton stand (Table 15). All (100.0%) members of the lodgepole pine stand were members of Group 1. The univariate F

statistics for the five groups showed significant differences among groups for a number of variables (Table 16). β-phellandrene exhibited the largest significant F-ratio among groups, followed by spine length, α-pinene, and needle length.

Discriminant analysis of the five groups produced four discriminant functions based on 16 variables, of which four were monoterpenes (Table 17). In the first discriminant function, which accounted for 75.6% of the total variation, α-pinene, needle length, and β-phellandrene displayed the largest loadings. In the second discriminant function, which accounted for 13.1% of the total variation, α-pinene, the cone bulge length/cone width ratio, and β-phellandrene had the heaviest loadings. The percentage of the original 178 individuals which were correctly classified with the discriminant functions was 100% for lodgepole pines, and averaged 97.8% for all individuals (Table 18).

All stands--5 variables. Principal component analysis of the 5 variables for all stands yielded two factors which accounted for 76.9% of the variation in the original data (Table 19). The first factor accounted for 51.3% of the original variation, with high loadings on α-pinene, β-phellandrene, and myrcene. The second factor accounted for 25.7% of the total variation, with high loadings on β-pinene and 3-carene. The separation between the lodgepole pine stand and the other three stands was less pronounced with the 5 character analysis than in the 22 character analysis, yet that separation remained distinct (Figure 11--Figure 8). Based upon monoterpene

composition alone, it was apparent that the putative hybrid stands more closely resembled the jack pine stand than the lodgepole pine stand.

The similarity coefficients from the first relocate cluster analysis suggest a four cluster solution (Figures 12 and 13). Analysis of the four cluster solution showed that groups 1 and 2 contained 98.6% of the Hinton lodgepole pines, while groups 3 and 4 contained mixtures of the jack pine and putative hybrid stands (Table 20). Four individuals from the Devon stand were included in groups 1 and 2 with the Hinton lodgepole pines. A single Hinton lodgepole pine was included in group 3.

Univariate F tests on the four groups showed α-pinene and β-phellandrene differed among the groups with the greatest significance (Table 21). Of particular interest was group 4, which displayed lower α-pinene and higher myrcene concentrations than the putative hybrid stand means. Also, group 2 possessed higher β-pinene and lower myrcene concentrations than the Hinton lodgepole pine stand means.

Discriminant analysis of the four groups produced three discriminant functions based on all compounds except β-pinene (Table 22). The first and second discriminant functions loaded heavily on β-phellandrene, and α-pinene and β-phellandrene, respectively. The percent classification of the 257 individuals into the four groups, based on the derived discriminant functions, was 94.6% correct (Table 23). Correct classification for members of the lodgepole pine clusters (groups 1 and 2) averaged 92.0%. Three out of 29 individuals

in group 2 were misclassified as members of groups 3 and 4.

The putative hybrid stands--22 variables. Principal component analysis of the 22 variables for the two putative hybrid stands at Onoway and Devon produced 9 factors which accounted for 81.0% of the total variation in the original data (Table 24). The first two factors accounted for 17.7% and 13.0%, respectively, of the total variation. The first factor showed complex loading with bulge length/cone length ratio, bulge length, and bulge length/cone width ratio displaying the heaviest loadings. Likewise the second factor was complex, with α-pinene and myrcene displaying heavy loadings. A graph of the first two principal component axes did not show distinct clusters (Figure 14).

The graph of the similarity coefficients was inconclusive in the selection of an appropriate number of groups (Figure 15). Four groups were selected for comparison with a subsequent four group solution of the 5 variable data for the hybrid stands (Figure 16). The allocation of individuals from the two stands to the three groups was roughly equal (Table 25). The univariate F statistics indicated that bulge spine length, bulge length/cone width ratio, bulge length, and bulge length/cone length ratio were the most significantly different variables among the groups (Table 26). Group 4 was of considerable interest, since its members possessed lower α-pinene concentrations, higher 3-carene concentrations and longer spines, compared to the other groups.

Discriminant analysis produced three discriminant functions

based on 14 variables, of which two were monoterpenes (Table 27). The first function accounted for 99.4% of the variation, and loaded heavily upon spine length and needle length/needle width ratio. The second function loaded heavily on bulge length/cone length ratio. The percent classification of the 94 individuals into the four groups averaged 98.9% correct (Table 28).

The putative hybrid stands--5 variables. The principal component analysis for the putative hybrid stands utilizing only the 5 variable (monoterpene) data accounted for 76.0% of the original variation in two factors (Table 29). The first factor accounted for 44.9% of the original variation with heavy loading on α-pinene. The second factor accounted for 31.1% of the original variation, with heavy loading on 3-carene and β-pinene. A graph of the two factor axes showed no distinct clusters containing a majority of members from any one stand (Figure 17).

The graph of the similarity coefficients (Figure 18) from cluster analysis suggested a four cluster solution (Figure 19). Membership for the four groups showed roughly equal representation of the Onoway and Devon stands in groups 1 and 2 (Table 30). Members of the Onoway stand accounted for 80.0% of group 3, while members of the Devon stand accounted for 91.3% of group 4. The univariate F statistics showed highly significant differences in β-phellandrene, 3-carene, and α-pinene among the four groups (Table 31).

Discriminant analysis produced three discriminant functions

(Table 32). The first function loaded heavily upon β-phellandrene; the second function loaded on 3-carene. The percent classification averages 97.52% correct with 3 misclassifications among 121 individuals (Table 33).

The Monoterpene Survey

A discriminant analysis between the Hinton lodgepole pine stand and the Cold Lake jack pine stand was performed on the α-pinene, β-pinene, 3-carene, and β-phellandrene variables. A single discriminant function was derived (Table 34). The function displayed heavy loadings on α-pinene and β-phellandrene. This function was used to classify the 592 members of the 14 stands (Table 35).

Two stands--Two Creeks and Twin Lakes--when classified showed high percentages of both lodgepole pine and jack pine. The discriminant function scores of all individuals from these stands, together with the Hinton and Cold Lake individuals, were plotted. There were a large number of intermediate trees, together with relatively pure jack and lodgepole pines (Figure 20).

IV. DISCUSSION

A. The Identification of Lodgepole Pine in the Population Study

Examination of the five groups from the 22 variable analysis of all stands in the population study showed that all Hinton lodgepole pines were contained in group 1. On the basis of the 22 characters, members of the putative hybrids were more closely related taxonomically to the jack pines at Cold Lake than to the lodgepole pines at Hinton (Figure 8). The strength of this relationship is apparent from the group means and the 100% success in the identification of lodgepole pine as members of group 1 in the discriminant analysis (Table 16).

Those characters with the largest significant F-ratios which distinguished the lodgepole pine from the other groups included higher concentrations of β-phellandrene, longer umbo spines, lower concentrations of α-pinene, longer needles, and acute umbo spine angles (Table 16).

The 5 variable (monoterpene composition) analysis of all stands in the population study produced a less pronounced but still distinct separation of lodgepole pine from members of the jack pine and putative hybrid stands. Of the 72 individuals in the lodgepole pine stand, 98.6% were placed in groups 1 and 2; only one was misclassified into one of the other two groups (Table 20). One and three members of the Devon population were placed in groups 1 and 2, respectively. It was noted, however, that subsequent validation of

the discriminant functions rejected the four Devon individuals as lodgepole pines. Evidently these trees represent borderline cases, which were subsequently rejected from cluster membership by the discriminant analysis.

The mean monoterpene composition of lodgepole pines at Hinton was 7.96% α-pinene, 11.27% β-pinene, 2.62% myrcene, 20.79% 3-carene, and 57.36% β-phellandrene (Table 6). The mean composition for the jack pine stand at Cold Lake was 75.67% α-pinene, 10.76% β-pinene, 0.01% myrcene, 13.22% 3-carene, and 0.34% β-phellandrene. The monoterpene compositions of the putative hybrid and jack pine stands are nearly identical, except for higher concentrations of β-phellandrene, and lower concentrations of β-pinene in the putative hybrid stands. Jack pine typically possesses much higher concentrations of α-pinene than does lodgepole pine. Similarly, β-phellandrene occurs in much higher concentrations in lodgepole pine than in jack pine. The concentration of 3-carene is 50% higher in lodgepole pine than in the other three stands.

Within the lodgepole pine stand, there are two distinct chemical types (Table 21). The most common type contains 7.33% α-pinene, 6.89% β-pinene, 2.12% myrcene, 26.15% 3-carene, and 57.51% β-phellandrene. The less common type contained 13.23% α-pinene, 18.34% β-pinene, 3.53% myrcene, 11.72% 3-carene, and 53.18% β-phellandrene.

The elimination of 17 morphological characters from the analysis did not greatly reduce the discrimination of the lodgepole pines from the other pines. There are good arguments for using monoterpenes

alone. A major consideration is that the discriminant functions in the 22 variable analysis loaded heavily upon six characters in the first two axes. Four of these characters were monoterpenes, and in each function the variable with the heaviest loading was a monoterpene. These loadings are indicative of the discriminating power of the monoterpenes as compared with morphology alone. Furthermore, the subsequent section will show that the inclusion of the morphological variables in the analysis of the putative hybrid stands actually may have obscured the population structure. When the morphological variables were eliminated, the identification of a group of suspected hybrids was possible.

B. The Identification of Hybrids in the Putative Hybrid Stands

Examination of the 22 variable analysis of the putative hybrid stands, unlike the 22 variable analysis of all stands, showed large loadings on a number of morphological characters in the first axis, and large loadings on the monoterpenes in the second axis. Four morphological characters exhibited the largest significant F-ratios among the four groups from cluster analysis (Table 26). The linear increase in the similarity coefficient as the number of clusters decreased during cluster analysis indicated that the distribution of individuals was continuous with only indistinct natural groupings (Figure 15).

Results from analysis of the 5 variable data for the putative hybrid stands were more conclusive. All five monoterpenes showed

significantly different concentrations among the four groups. In an attempt to identify these groups, hypothetical monoterpene compositions were calculated from the Hinton and Cold Lake stands for F_1 hybrids, and backcrosses from the F_1 to each parental stand (Table 36). Additivity of monoterpene composition was assumed, despite contradictory evidence in the form of strong bimodal distributions in several compounds. The third group contained 10 individuals with an average monoterpene composition within 5% of all monoterpene concentrations for a hypothetical backcross of an F_1 hybrid to jack pine (Table 31). A single individual in the Devon stand possessed 40.5% α-pinene, 7.2% β-pinene, 2.2% myrcene, 25.1% 3-carene, and 25.1% β-phellandrene, which would correspond to a hypothetical F_1 hybrid. No individuals were found which corresponded to hypothetical F_1 backcrosses to lodgepole pine.

The other three groups from the cluster analysis of the putative hybrids closely resembled the Cold Lake jack pine chemically. The formation of these groups during cluster analysis appears to have been caused by the bimodal distributions of β-pinene and 3-carene. These compounds exhibited similar distributions in the Cold Lake population. Thus, these three groups are assumed to be typical of the parental jack pines.

It was difficult to confirm the identity of any suspected hybrids and hybrid derivatives using existing research. Close examination of work of Zavarin et al. (1969) showed that nearly all of the hybrids produced at the Institute of Forest Genetics had Sierra-Nevada lodgepole pine parents. No analyses of monoterpene composition

were performed on the jack pine parents, as they had died before the study. Since the monoterpene composition of the Sierra-Nevada race of lodgepole pine differs from the Rocky Mountain race, the results of Zavarin et al. (1969) are not valid estimates for crosses of Alberta lodgepole pine and jack pine sources. Mirov (1956) also used hybrids at the Institute of Forest Genetics; again, many of the parental trees were not from local sources.

Without controlled crosses from local sources, the exact identification of hybrids in natural stands will remain imprecise. The suspected hybrids of group 3 in the analysis of the putative hybrid stands were identified on the basis of hypothetical information and remain untested.

Despite these difficulties with the identification of hybrids, the practical identification of lodgepole pine is considerably easier. Both Mirov (1956) and Zavarin et al. (1969) found that some aspects of jack pine monoterpene composition--specifically α-pinene concentration--exhibited dominance in F_1 hybrids. Zavarin et al. found that monoterpene composition of the F_1's averaged 70% pinenes and 24% β-phellandrene, while Mirov detected 75% to 78% pinenes and 20% to 22% β-phellandrene. This dominance would cause the monoterpene compositions of a majority of hybrids and hybrid derivatives to grossly resemble jack pine except for a noticeably higher β-phellandrene concentration.

From a practical tree improvement standpoint, the classification of a tree as either lodgepole pine or a member of the jack pine-hybrid group is not difficult. It would be relatively easy to

separate lodgepole pine from the combined group of jack pine and the hybrids, but it would be quite difficult to distinguish between jack pine and the hybrids in this latter group. The most accurate approach for identifying hybrids in natural pine stands would use discriminant analysis. Plots of the discriminant scores of individuals in stands could indicate the presence of variants and the degree of hybridization along a pure jack pine-pure lodgepole pine scale (Figure 20). The hybrids which resembled jack pine could be classified as jack pine and immediately eliminated, but those hybrids which resembled lodgepole pine would have to be evaluated on the basis of their discriminant scores. Individuals which showed strong tendencies toward intermediacy could be eliminated. A cutoff score to separate pure lodgepole pine from lodgepole-like hybrids cannot be determined objectively without a series of controlled backcrosses to lodgepole pine.

C. The Distribution and Nature of Hybridization in Alberta

The Active Hybridization Zone

Since we know the gross monoterpene composition of an F_1 as determined by previous research, and if one assumes that the average monoterpene composition of a stand accurately represents the gross species composition of that stand, isoconcentration maps can be utilized to locate the active hybridization zone. In such a zone, large numbers of both jack pine and lodgepole pine chemical types would be found together in many of the local stands. Since the ease of hybridization between the two species has been well established, it is likely that hybridization will occur in a mixed stand of jack

and lodgepole pine.

In the analyses, β-pinene and β-phellandrene were the most important vaiables in the discrimination between lodgepole pine and the group of jack pine and the putative hybrids. Isoconcentration maps of these compounds show a high gradient region to the west of the hybridization region reported by Moss (1949) and Mirov (1956) (Figures 4 and 7). The region appears continuous from Rocky Mountain House to the northwestern corner of the province, but it should be stressed that pine stands in northwestern Alberta often are isolated. None of the upland populations in areas such as the Caribou Mountains were sampled in this study. Thus, the active hybridization zone in northwestern Alberta may be more complex than indicated on the isoconcentration maps.

The existence of mixed stands in the active hybridization zone can be established by examining the discriminant classifications from the monoterpene survey. At the Rocky Mountain House, Two Creeks, and Twin Lakes stands, 20.6%, 37.5%, and 42.1% of the trees were classified as jack pines on the basis of their monoterpene composition (Table 35). Plots of the discriminant scores of the Two Creeks and Twin Lakes stands show that stands in the active hybridization zone are not simple mixtures of pure jack pine and pure lodgepole pine monoterpene types; they contain large numbers of hybrid monoterpene types as well (Figure 20). The much greater variation in monoterpene composition in them closely resembles what one would expect of F_2 or F_2-backcross bybrids.

Interestingly enough, the putative hybrid stands used in the

population study are not located within the active hybridization zone, but lie just beyond its eastern boundary. These stands contain a number of suspected F_1 backcrosses to jack pine and a single suspected F_1 at Devon which were found during discriminant analysis of the monoterpenes (Table 35). This raises an important question. The isolation of these stands would prevent direct hybridization between jack and lodgepole pine. How, then, did these suspected hybrids get established in the Devon and Onoway stands?

The Presence of Variant Individuals Outside the Zone of Active Hybridization

Besides the evidence of a small group of variant individuals in the putative hybrid stands of the population study, there was additional evidence of gene flow beyond the zone of active hybridization in the Hinton stand and the monoterpene survey. At Hinton, far from any jack pine stands, a single jack pine chemical type (77.8% α-pinene) and two other individuals with more than 30.0% α-pinene were noted. The results of the discriminant classification of the 14 stands in the monoterpene survey showed low but consistent percentages (2.6% to 4.0%) of jack pine chemical types in lodgepole pine stands from Lake Abraham to Canmore (Table 35).

The absence of any jack pine chemical types in the Cypress Hills stand was additional evidence that we are not dealing with variant chemical types typical of pure lodgepole pine stands and unconnected to gene flow from jack pine. If such variants are typical of pure lodgepole pine stands, they should occur in the Cypress Hills. That they do not occur can be explained by either

of two hypotheses. First, Cypress Hills may represent a pure population of lodgepole pine which has never crossed with jack pine. Since the Front Range stands contain a small percentage of the variant types, it is likely that the Cypress Hills population was established and isolated prior to the range overlap of the two species.

A second explanation for the absence of variants in the Cypress Hills is the founder effect. It is conceivable that this outlier population was established by one or a very few migrant trees. In such a case, there would be a low probability that these founders would contain the less common variant genes, and a high probability that the founders would contain genes for typical lodgepole pine monoterpene composition.

Any explanation of the presence of these variants in the putative hybrid stands, the Hinton lodgepole pine stand, and the Front Range lodgepole pine stands, must consider gene flow of some form between the species. At least in the putative hybrid stands, these variant trees are atypical of the jack pine stand at Cold Lake. One explanation for the presence of these variants at Onoway and Devon would be former range extensions of both jack pine and lodgepole pine. It is possible that the range of lodgepole pine may have extended further to the east in the past. Adjacent or intermixed stands of lodgepole and jack pine could have existed at Onoway and Devon, with ensuing hybridization. At some time climatic conditions changed, and the range of lodgepole pine receeded westward. If that was the case, lodgepole pine genes controlling monoterpene composition may have been maintained in the Onoway and Devon populations for

hundreds or possibly thousands of years in the absence of any active hybridization. This explanation may be reasonable enough to explain the presence of variants in the putative hybrid stands, but it is not reasonable to suggest that the variants in the lodgepole pine stands at Coleman were caused by a similar former southern range extension of jack pine.

A second possible explanation is introgression. This mechanism would allow lodgepole pine genes to move through an area of hybridization and into the range of jack pine beyond the eastern limit of lodgepole pine. If introgression has occurred, the prior presence of lodgepole pine at Onoway and Devon would not be necessary to explain the presence of the variant trees.

Introgression has been studied or suspected in a number of cases involving tree species (Muller 1952, Cooperrider 1957, Dugle 1966, Benson et al. 1967, and Roche 1969). Anderson (1949) described the process as the incorporation of genes or gene complexes of one species into another species via hybridization and subsequent migration of the genes by backcrossing away from the zone of hybridization. He suggested that since the parental species are optimally adapted to specific sites, any interspecific hybrids will be capable of successful competition and establishment only on intermediate sites. Muller (1952) described Texas hybrids between Quercus harvardi Rydb. and Q. mohriana Buckl. which occupied the intermediate zones between the deep sand preferred by Q. harvardi and the exposed limestone preferred by Q. mohriana.

In his theory, Anderson stated that as one left the center

of a hybrid swarm and moved toward the range limit of a parental species, a cline of variation would be observed. Individuals in the center of the hybrid swarm would display predominantly intermediate characters, whereas individuals on the edges of the hybridization area would resemble one or the other parental species. Such clines could be attributed to the varying frequency of backcrossing and the changing environmental selection pressures which would occur as one moved through the hybridization area. As the limit of the hybrid swarm was approached, and as site conditions progressively resembled those conditions favored by one or the other parental species, any hybrid derivatives with adaptive traits more similar to that parental species would have higher fitness and would predominate on those sites. Benson et al. (1967) described such sorting of characters in a hybrid swarm between Quercus Douglasii Hook. & Arn. and Q. turbinella Greene subsp. californica Tucker. There were measurable differences in morphology on adjacent slopes separated by as little as 45 degrees in aspect. Thus, within the zone of hybridization, individuals were sorted by site conditions and tended to resemble a single parental species, whenever site conditions resembled the conditions favored by either of the parental species.

Successful backcrossing by the hybrids to one or both of the parental species is required if such a cline is to become established. Backcrossing also constitutes the mechanism by which the genes of one species can become incorporated into the genome of another species. If introgression is suspected, anomalous patterns of variation should be found in the parental stands beyond the zone

of hybridization. The frequency of variant individuals in the parental stands should decrease as one moves farther away from the hybridization zone and the influence of introgression becomes less.

Anderson's test for introgression was an examination of parental populations beyond the hybridization zone. In this study the Cypress Hills stand did not contain individuals with variant jack pine monoterpene composition, whereas the less isolated lodgepole pine stands along the Front Range did contain such variants. Plots of the discriminant scores of the Hinton, Cold Lake, Two Creeks, and Twin Lakes stands showed the higher frequencies of the variants in the active hybridization zone than in the stands beyond the zone (Figure 20). Also, variants were found in the putative hybrid stands, though not at Cold Lake. This evidence suggests that the variants are not representative of the normal variation found in pure stands of lodgepole pine and jack pine. Likewise, it is unlikely that the range of jack pine ever extended to the Crowsnest Pass area at Coleman. The most plausible explanation which explains the presence of atypical variants in these populations is the introgression theory.

Evidence supporting a recent overlap in the ranges of the two species can be found in the isoconcentration maps of α-pinene and β-phellandrene. Both show steep, high gradient clines just east of the Front Range. Ancient range extensions of any scale would have blurred and broadened such gradients.

Despite this evidence in support of the introgression theory, it should be stressed that the situation in Alberta differs

considerably from the cases mentioned by Anderson (1949). Anderson dealt with well defined parental species occupying different sites. Intermediate hybrids bridged the parental isolation to allow back-crossing and subsequent gene flow into the parental species. In Alberta, however, two poorly differentiated species capable of occupying similar sites have undergone a recent range overlap, subsequent hybridization, and gene flow between the two species.

Also, the lack of monoterpene variants in the Cold Lake population cannot be construed as prima facie evidence that introgression of lodgepole pine genes into jack pine populations has not occurred. Given that introgression of each species occurred at the same rate into the other species, the frequency of high pinene variants in the lodgepole pine stands would be considerably higher than the frequency of high phellandrene variants in the jack pine stands, due to the previously mentioned dominance of some aspects of jack pine monoterpene composition.

D. Comments on the Evolutionary Differentiation of Pinus Contorta and Pinus Banksiana

The fact that lodgepole pine and jack pine are not good biological species is evident from the many instances of their putative natural and artificial crossings which produced viable offspring (Moss 1949, Righter and Stockwell 1949). Nonetheless, there is some evidence that the two species have begun to differentiate reproductively. Both Moss (1949) and Saylor and Smith (1966) noted 50% and 31% pollen abortion respectively in natural and artificial hybrids.

These data would indicate the beginnings of reproductive incompatibility, although not the full reproductive isolation necessary for continued differentiation of (at least in central Alberta) adjoining populations.

A possible explanation for the obvious morphological differentiation and partial reproductive differentiation can be found in an examination of the paleo-geography of these species. While there is considerable debate concerning the location of the Wisconsin glacial refugia for lodgepole and jack pine, most authors agree that at least two refugia existed (Yeatman 1967, Ritchie 1976). One refugium of jack pine was located on the coast and continental shelf of what is now the southeastern United States, with the possibility of a second jack pine refugium in the Yukon. A lodgepole pine refugium was located on the coast of British Columbia. The inclusion of both species in the same refugium would be unlikely, since lodgepole pine and jack pine prefer similar well-drained sites. Lodgepole pine and jack pine in the same refugium likely would have interbred.

Thus, the differentiation between jack and lodgepole pine probably was tied intimately to the periodic geographic isolation of several populations in glacial refugia. In view of the glacial history of North America and fossil evidence, it is probable also that the ranges of jack pine and lodgepole pine have overlapped during previous interglacial periods (Yeatman 1967). To date none of the periods of geographic isolation between the interglacials have been sufficient to allow the sexual isolation of the two

populations. Rather, geographic isolation has permitted distinct morphological differentiation with enough changes in the genes of the two "species" that incompatibilities show up during hybrid pollen development. Despite these differences, we do not as yet have the "genetic revolution" described by Mayr (1963) in his theory of geographic isolation and subsequent speciation. Rather, we have two poorly differentiated species which have recently renewed an ancient but as yet incomplete association.

V. CONCLUSIONS

In the course of this study, it was found that distinct groups, as defined by morphology and xylem oleoresin monoterpene composition, can be found in Alberta's natural pine stands with the use of techniques of principal component, cluster, and discriminant analysis. Among the population study stands, it was possible to identify one group as lodgepole pine using either all 22 characters or just the five monoterpene characters. With 22 characters in the putative hybrid stands, the identification of distinct groups was difficult due to a continuous distribution of individuals. When only five monoterpene characters were used in the analysis of the putative hybrid stands, a group was found containing suspected F_1 backcrosses to jack pine.

It was found that lodgepole pine can be separated from jack pine and the putative hybrids on the basis of either both morphological and chemical characters or solely on chemical characters. In the analysis of 22 variables, α-pinene, β-phellandrene, and needle length were the most important characters for separating lodgepole pine from the putative hybrids and jack pine. The lodgepole pines at Hinton had needles which averaged 59.7 mm in length versus the 32.6 mm to 36.0 mm in the two putative hybrid stands and the single jack pine stand. The concentration of α-pinene in the Hinton stand averaged 7.96% versus 72.96% to 75.67% in the other three stands. Finally, the concentration of β-phellandrene in the Hinton stand averaged 57.36% versus 0.34% to 3.04% in the other stands.

In the analysis of the monoterpene composition alone, α-pinene and β-phellandrene concentrations were the most important characters for identifying lodgepole pine. It was noted that morphology was not related consistently to monoterpene composition within a stand, especially in the lodgepole pine stand where two chemically variant trees were found. The monoterpene composition of one tree resembled a putative hybrid, and the monoterpene composition of the other tree was identical to a jack pine. Both trees possessed typical lodgepole pine morphology. Discrimination by 22 variable analysis would have classified these individuals as lodgepole pines owing to the masking effects of other morphological variables. Accordingly, it is recommended that the monoterpene composition of the xylem oleoresin be used to distinguish between lodgepole pine and the combined jack pine-hybrid pine group. Monoterpene data from a lodgepole pine stand such as the one at Hinton, and a jack pine stand such as the one at Cold Lake, can be used to construct discriminant functions to classify trees along a scale between lodgepole pine or jack pine. Since the genes which control the monoterpene composition of jack pine are dominant, many introgressants in lodgepole pine stands will be classified as jack pine because they resemble jack pine chemically. Other, more intermediate individuals can be detected by their intermediate discriminant function scores. Both types of individuals can be eliminated, if desired, from a tree improvement program.

Gas chromatography can provide the necessary information on monoterpene composition for the discriminant classification of a tree. Four monoterpenes--α-pinene, β-pinene, 3-carene, and

β-phellandrene--should be analyzed in the xylem oleoresin. Myrcene, since it is a trace compound, should be ignored because it drops out of the analysis occasionally due to changes in operating conditions.

The zone of active hybridization in Alberta has been mapped using the average monoterpene concentrations of stands. The isoconcentration maps of α-pinene and β-phellandrene (Figures 4 and 7) show an area of high gradient to the west of the previously described hybridization area (Moss 1949 and Mirov 1956). Apparently this zone is continuous from Rocky Mountain House to the northwestern corner of the province. Within this zone, stands contained large percentages of jack pine, lodgepole pine, and hybrid chemical types. This zone of active hybridization, since it is based on average monoterpene concentrations in a stand, does not indicate the introgressants which occur in stands beyond the zone. Such introgressants can be identified on the basis of their discriminant scores.

VI. RECOMMENDATIONS

The monoterpene composition of xylem oleoresin can be used to identify jack pine genes in lodgepole pine trees. Individuals considered for mass selection and breeding could be tested using gas chromatography and discriminant analysis to eliminate trees which contain jack pine genes. Owing to differences in g.c. techniques, it would be most accurate if a forest geneticist repeated parental type sampling at relatively pure stands such as the Hinton and Cold Lake stands. The use of normalized percentages would not be required for such a program; area percentages would be sufficient. If large numbers of g.c. analyses are performed, adjustment for varying detector response should be made by repeating a standard sample every 10 to 20 analyses, and correcting for drift. While α-pinene and β-phellandrene are the most important compounds for differentiating between lodgepole pine and jack pine and the hybrids, g.c. analysis will provide percentages for all compounds. As myrcene is a trace monoterpene which occasionally drops below the detection limit, analysis only of the four major monoterpenes--α-pinene, β-pinene, 3-carene, and β-phellandrene--is recommended. These data can be used to derive a discriminant function, which could be used to classify individual trees as either lodgepole pine or jack pine. Due to dominance of jack pine monoterpenes, many hybrids will be included in the jack pine category. Hybrids with predominately lodgepole pine characteristics can be detected by their intermediate discriminant scores.

A number of the monoterpenes, specifically α-pinene, β-pinene, 3-carene, and β-phellandrene, showed distinctive bimodal frequency distributions in the population study stands. If, as is likely, these distributions are caused by simple Mendelian genes, up to 16 different monoterpene genotypes are possible. The identification and determination of the frequencies of these genotypes in natural stands is suggested, since they have practical applications in tree improvement programs. Homozygous monoterpene genotypes have been used in slash pine (Squillace 1977) to measure outcrossing and foreign pollen contamination in seed orchards. It is suggested that two large samples of 1000 individuals be collected in the Hinton and the Cold Lake areas to identify and determine the frequency of various monoterpene genotypes in relatively pure stands of each species.

In addition, controlled crosses from local sources should be made to determine the inheritance of monoterpenes and to identify the exact characteristics of various hybrids and hybrid derivatives. This work would allow more precise identification of hybrids, and their eventual separation from the jack pine monoterpene types. Controlled backcrosses of hybrids to lodgepole pine would allow an objective cutoff to be determined for a discriminant function such that lodgepole-like hybrids could be separated from pure lodgepole pine.

VII. TABLES

Table 1. Morphological characteristics of *Pinus contorta* var. *latifolia*, *P. banksiana*, and the putative hybrids in Alberta (after Moss 1949 and Mirov 1956).

Character	Taxon		
	P. contorta var. *latifolia*	putative hybrids	*P. banksiana*
Habit	-tall, straight clean trunk -ends of branches sweep upward in wide-crowned trees	-intermediate	-wide crown -scrubby growth -branches may droop
Bark	-darker color -finer, more uniform scales -loosely appressed scales	-unknown	-lighter -irregular scaly ridges and furrows
Foliage	-needles in two's - 1 to 3" long -less divergent -less twisted -more dense clusters	-in two's -similar to *P. banksiana*	-in two's -1 to 1½" long -divergent -twisted
Pollen	-shed later than *P. banksiana* -few grains distorted	-shed later than *P. banksiana* -50% distorted	- shed earler than *P. contorta* -few grains distorted
Female Cones	-armed -spreading at obtuse angles -linear cones	-highly variable curvature and orientation -minutely armed -resembles *P. contorta*	-unarmed -erect at acute angles -curved cones

Table 2. Variable definitions and descriptions.

Variable	Description
1	needle length in mm.
2	needle width in mm.
3	needle length/needle width ratio.
4	cone angle (ABC in Figure 4) in degrees.
5	cone curvature (DE/BC) ratio.
6	umbo bulge height (FG/HI).
7	spine length (JK) in mm.
8	spine angle (XJK) in degrees.
9	maximum cone length (CL) in mm.
10	maximum cone width (BL) in mm.
11	bulge length (LM) in mm.
12	bulge angle (NOP) in degrees.
13	cone length/cone width ratio.
14	bulge length/cone width ratio.
15	bulge length/cone length ratio.
16	cone angle, corrected for cone curvature, in degrees.
17	percentage of physically aborted pollen grains.
18	α-pinene, normalized percentage.
19	β-pinene, normalized percentage.
20	myrcene, normalized percentage.
21	3-carene, normalized percentage.
22	β—phellandrene, normalized percentage.

Table 3. Location of the 14 study sites.

No.	Name	Longitude	Latitude	Elevation	Notes
1	Hinton	117° 29'	53° 26'	1170 m.	- morphologically pure *P. contorta*
2	Onoway	114° 9'	53° 44'	710	- morph. hybrids and *P. banksiana*
3	Devon	113° 44'	53° 24'	705	- morph. hybrids and *P. banksiana*
4	Cold Lake	110° 14'	54° 27'	535	- morph. pure *P. banksiana*
5	Cypress Hills	110° 17'	49° 39'	1410	- morph. pure *P. contorta*
6	Coleman	114° 30'	49° 45'	1090	- morph. pure *P. contorta*
7	Canmore	115° 17'	51° 6'	1630	- morph. pure *P. contorta*
8	Lake Abraham	116° 27'	52° 15'	1750	- morph. pure *P. contorta*
9	Rocky Mt. House	115° 3'	52° 21'	1000	- morph. pure *P. contorta*
10	Two Creeks	116° 18'	54° 18'	920	- morph. pure *P. contorta*
11	Peace River	117° 14'	56° 13'	340	- morph. hybrids and *P. banksiana*
12	Twin Lakes	117° 32'	57° 4'	650	- morph. pure *P. contorta* in muskeg
13	Chinchaga River	118° 20'	58° 35'	370	- morph. hybrids, 27 m. tall
14	Ft. Vermillion	116° 15'	58° 19'	280	- morph. pure *P. banksiana*

Table 4. Gas chromatograph operating conditions.

Temperatures:	
- injection port:	165 degrees C.
- column oven:	45 degrees C.
- flame ionization detector:	175 degrees C.
Carrier gas:	Helium
Flow Rate:	25 ml per minute
Detector:	Flame ionization
Sample size:	1 µl, liquid.
Analytical column:	6' by 0.125" 3% SE-30 on Chromosorb W, Non-acid washed, 60/80 mesh
Standards:	external every 10 runs

Table 5. Multivariate analyses in the population study.

Data Subsets:

1). The Hinton stand (*Pinus contorta* var. *latifolia*).
2). The Onoway stand (putative hybrids).
3). The Devon stand (putative hybrids).
4). The Cold Lake stand (*Pinus banksiana*).

Data Combinations:

1). All individuals in all four stands, 22 variables per individual.
2). All individuals in all four stands, 5 variables per individual.
3). All individuals in the putative hybrid stands (Onoway and Devon), 22 variables per individual.
4). All individuals in the putative hybrid stands (Onoway and Devon), 5 variables per individual.

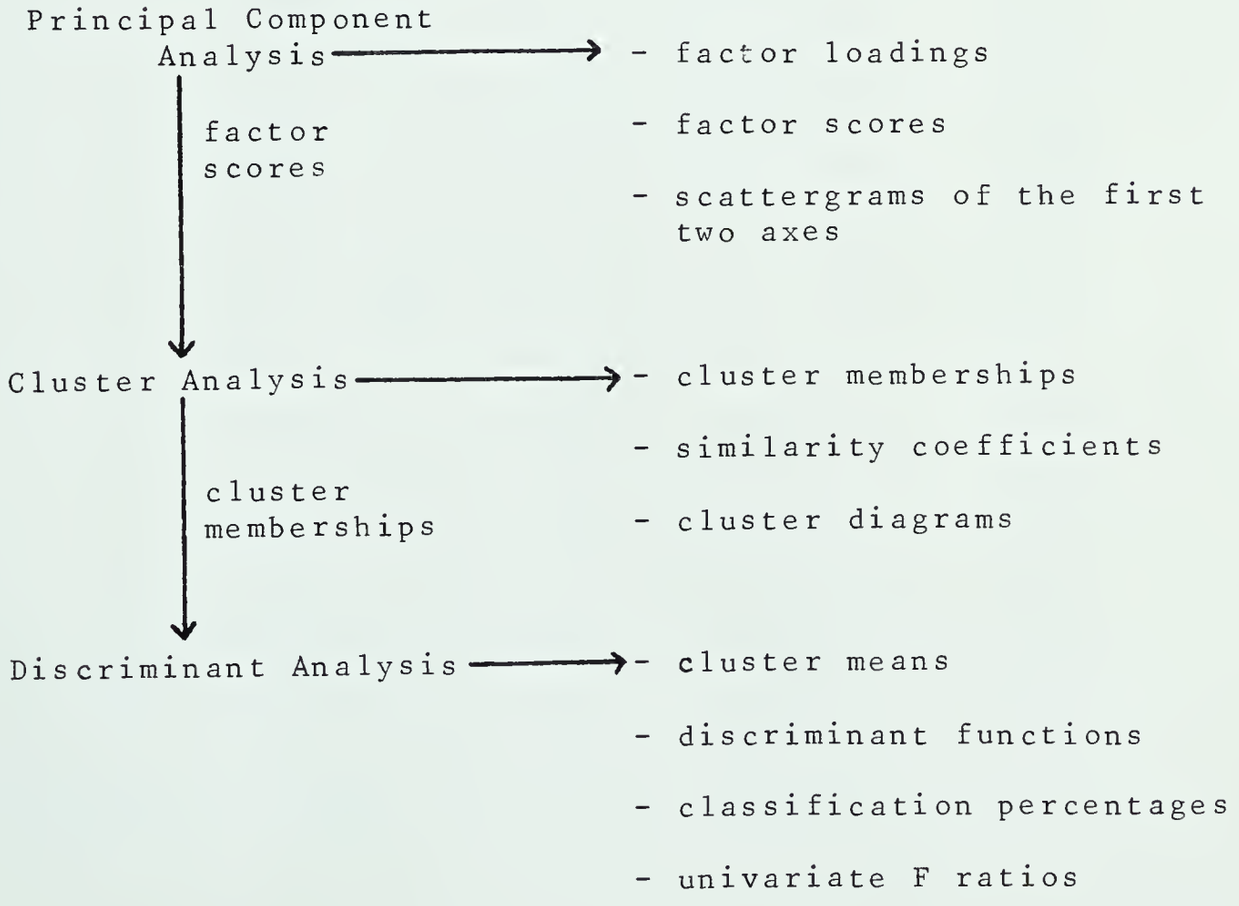

Table 6. Means of all characters of pines in the population study stands

Variable	Hinton	Onoway	Devon	Cold Lake
1	59.7 mm	36.4	32.6	33.2
2	1.30 mm	1.37	1.34	1.47
3	46.3	27.2	24.5	22.6
4	119. deg.	33.	33.	6.
5	0.02	0.15	0.12	0.20
6	2.9	5.1	5.2	4.7
7	1.8 mm	0.6	0.5	0.6
8	62. deg.	161.	168.	156.
9	43.5 mm	40.7	42.4	41.2
10	25.3 mm	21.3	20.2	22.6
11	21.2 mm	19.6	20.4	28.4
12	139. deg.	161.	159.	182.
13	1.73	1.93	2.10	1.83
14	0.82	0.91	1.00	1.25
15	0.48	0.50	0.48	0.70
16	128. deg.	99.	85.	91.
17	3.7 %	2.3	3.6	1.3
18	7.96 %	75.25	72.96	75.67
19	11.27 %	6.50	9.94	10.76
20	2.62 %	1.39	1.82	0.01
21	20.79 %	14.91	12.23	13.22
22	57.36 %	1.96	3.04	0.34

Table 7. Univariate statistics for the Hinton stand.

Variable	Mean	Minimum	Maximum	S.D.	S.E.	Kurtosis	Skewness
1	59.7	43.0	79.3	7.62	10.87	-0.265	0.293
2	1.30	1.01	1.77	0.14	0.017	0.133	0.476
3	46.3	33.5	63.1	6.01	0.685	0.125	0.469
4 *	119.	42.0	153.	22.5	2.58	2.29	-1.69
5 *	0.02	0.00	0.11	0.03	0.004	0.78	1.4
6 *	2.9	1.0	5.0	0.81	0.092	0.49	0.11
7 *	1.8	0.0	3.0	0.55	0.063	1.9	-1.0
8 *	62.	0.	125.	17.0	1.97	3.47	0.103
9	43.5	35.0	62.0	5.18	0.590	1.14	0.717
10	25.3	19.0	40.0	3.26	0.371	4.18	1.30
11 *	21.2	0.0	36.0	8.74	1.15	1.94	1.54
12 *	139.	0.	360.	61.3	8.04	3.42	-0.309
13	1.73	1.33	2.26	0.174	0.020	0.164	0.395
14 *	0.82	0.00	1.27	0.336	0.044	1.99	-1.61
15 *	0.48	0.00	0.75	0.194	0.025	2.08	-1.66
16	128.	42.	202.	22.8	2.68	3.54	-0.415
17 *	3.7	0.0	28.4	5.17	0.601	11.4	3.04
18 *	7.96	2.85	77.8	9.99	1.18	34.7	5.42
19	11.27	2.01	32.12	7.22	0.851	0.351	0.882
20 *	2.62	1.07	11.64	1.28	0.151	34.5	5.01
21	20.79	1.30	54.70	11.8	1.40	-0.027	0.494
22	57.36	3.58	83.17	13.7	1.61	2.98	-1.14

* indicates the rejection of a normal distribution by the Kolomogov-Smirnoff test ($\alpha = .05$).

Table 8 . Univariate statistics for the Onoway stand.

Variable	Mean	Minimum	Maximum	S.D.	S.E.	Kurtosis	Skewness
1	36.4	27.7	49.5	4.29	0.614	0.664	0.289
2	1.37	0.52	1.64	0.164	0.023	14.4	-2.78
3 *	27.2	20.0	69.6	7.00	1.00	28.9	4.78
4 *	33.	-17.	140.	46.5	6.64	-0.467	1.00
5	0.15	0.00	0.35	0.103	0.015	-1.17	-0.012
6 *	5.1	2.0	10.0	2.32	0.33	0.79	1.4
7 *	0.6	0.5	1.1	0.153	0.022	5.59	2.71
8 *	161.	135.	180.	22.5	3.21	-1.99	-0.298
9	40.7	24.0	56.0	5.67	0.810	1.12	0.110
10	21.3	14.0	28.1	2.63	0.375	0.917	0.223
11 *	19.6	0.00	41.2	14.6	2.08	-1.45	-0.431
12	161.	0.	360.	95.2	13.7	0.573	0.313
13	1.93	1.44	2.80	0.281	0.040	0.858	0.826
14 *	0.91	0.00	1.89	0.685	0.098	-1.49	-0.393
15 *	0.50	0.00	1.00	0.372	0.053	-1.47	-0.399
16	99.	30.	181.	33.3	4.75	-0.276	0.402
17 *	2.3	0.0	27.0	4.13	0.63	31.8	5.34
18	75.25	51.08	96.54	13.8	1.91	-1.34	-0.015
19	6.50	1.67	13.57	2.95	0.409	-0.457	0.465
20	1.39	0.68	2.46	0.445	0.062	-0.325	0.393
21 *	14.91	0.00	40.87	13.8	1.92	-1.38	0.198
22 *	1.96	0.00	23.37	4.55	0.631	18.22	4.32

* indicates the rejection of a normal distribution by the Kolomogov-Smirnoff test (α =.05).

Table 9. Univariate statistics for the Devon stand.

Variable	Mean	Minimum	Maximum	S.D.	S.E.	Kurtosis	Skewness
1	32.6	23.0	43.0	4.23	0.486	-0.388	0.222
2	1.34	1.05	1.69	0.111	0.013	0.523	0.389
3	24.5	18.5	31.6	0.342	2.98	-0.559	0.015
4 *	33.	-40.	113.	4.11	36.1	-0.648	0.382
5 *	0.12	0.00	0.64	0.013	0.113	5.06	1.64
6 *	5.2	2.1	9.9	2.27	0.26	0.68	1.4
7 *	0.5	0.4	1.0	0.12	0.01	11.	3.6
8 *	168.	90.	175.	21.5	2.47	0.823	-1.39
9	42.4	32.1	56.3	5.38	0.617	-0.413	0.262
10	20.2	16.0	29.3	2.69	0.326	1.27	0.986
11 *	20.4	0.0	43.2	12.4	1.54	-0.819	-0.676
12 *	159.	0.	360.	113.	14.1	-0.434	0.295
13	2.10	1.58	2.75	0.272	0.033	-0.058	0.416
14 *	1.00	0.00	2.06	0.609	0.076	-0.726	-0.679
15 *	0.48	0.00	0.92	0.294	0.037	-0.769	-0.688
16	85.	30.	208.	39.3	4.70	1.52	1.17
17 *	3.6	0.0	14.0	2.87	0.330	1.763	1.269
18	72.96	40.54	94.48	12.97	1.56	-0.412	-0.407
19	9.94	2.17	24.95	4.74	0.570	0.434	0.825
20 *	1.82	0.72	4.70	0.679	0.082	5.57	1.88
21	12.23	0.00	43.71	11.7	1.41	-0.388	0.686
22	3.04	0.00	25.07	4.83	0.581	9.805	3.19

* indicates the rejection of a normal distribution by the Kolomogov-Smirnoff test ($\alpha = .05$).

Table 10. Univariate statistics for the Cold Lake stand.

Variable	Mean	Minimum	Maximum	S.D.	S.E.	Kurtosis	Skewness
1	33.2	24.3	44.4	3.46	0.402	0.871	0.617
2	1.47	1.29	1.80	0.092	0.011	0.984	0.423
3	22.6	17.4	28.9	2.53	0.294	0.290	0.599
4 *	5.	-35.	120.	24.7	2.89	6.68	2.19
5	0.20	0.00	0.69	0.127	0.015	2.191	0.963
6 *	4.7	2.0	9.8	2.09	0.244	2.00	1.67
7 *	0.6	0.4	1.0	0.203	0.024	0.221	1.49
8 *	156.	95.	180.	25.0	2.92	-0.929	-0.363
9	41.2	31.0	52.3	4.64	0.543	-0.201	0.181
10	22.6	16.2	28.1	2.41	0.283	0.205	0.177
11 *	28.4	0.0	45.2	10.2	1.23	2.94	-1.70
12 *	182.	0.	360.	66.6	7.85	2.43	0.656
13	1.83	1.48	2.74	0.225	0.026	2.40	1.18
14 *	1.25	0.00	1.86	0.460	0.055	2.53	-1.58
15 *	0.70	0.00	1.00	0.256	0.031	2.49	-1.64
16	91.	18.	214.	33.9	3.99	1.76	0.933
17	1.3	0.0	4.8	0.93	0.12	2.24	1.19
18	75.67	48.55	99.99	13.23	1.65	-1.02	-0.127
19	10.76	0.01	30.21	5.80	0.726	1.49	1.07
20 *	0.01	0.00	0.51	0.069	0.009	44.1	6.37
21 *	13.22	0.00	44.94	13.23	1.65	-1.15	0.449
22 *	0.34	0.00	2.22	0.487	0.061	4.07	1.78

* indicates the rejection of a normal distribution by the Kolomogov-Smirnoff test ($\alpha = .05$).

Table 11. Kruskal-Wallis one-way analyses of variance with the Hinton stand.

Variable	Level of Significance		
	Onoway	Devon	Cold Lake
1	0.000*	0.000*	0.000*
2	0.001*	0.038*	0.000*
3	0.000*	0.000*	0.000*
4	0.000*	0.000*	0.000*
5	0.000*	0.000*	0.000*
6	0.000*	0.000*	0.000*
7	0.000*	0.000*	0.000*
8	0.000*	0.000*	0.000*
9	0.005*	0.200	0.008*
10	0.000*	0.000*	0.000*
11	0.331	0.528	0.000*
12	0.153	0.283	0.000*
13	0.000*	0.000*	0.006*
14	0.022*	0.000*	0.000*
15	0.051	0.161	0.000*
16	0.000*	0.000*	0.000*
17	0.147	0.117	0.006*
18	0.000*	0.000*	0.000*
19	0.000*	0.608	0.993
20	0.000*	0.000*	0.000*
21	0.016*	0.000*	0.000*
22	0.000*	0.000*	0.000*

* indicates a significant difference from the Hinton stand ($\alpha = 0.05$).

Table 12 . Kruskal-Wallis one-way analyses of variance with the Cold Lake stand.

Variable	Level of Significance		
	Onoway	Devon	Hinton
1	0.000*	0.330	0.000*
2	0.000*	0.000*	0.000*
3	0.000*	0.000*	0.000*
4	0.001*	0.000*	0.000*
5	0.042*	0.000*	0.000*
6	0.275	0.065	0.000*
7	0.334	0.141	0.000*
8	0.400	0.010*	0.000*
9	0.529	0.224	0.008*
10	0.003*	0.000*	0.000*
11	0.001*	0.000*	0.000*
12	0.073	0.075	0.000*
13	0.074	0.000*	0.006*
14	0.020*	0.012*	0.000*
15	0.005*	0.000*	0.000*
16	0.163	0.135	0.000*
17	0.142	0.000*	0.006*
18	0.925	0.306	0.000*
19	0.000*	0.492	0.993
20	0.000*	0.000*	0.000*
21	0.724	0.926	0.000*
22	0.000*	0.000*	0.000*

* indicates a significant difference from the Cold Lake stand ($\alpha = 0.05$).

Table 13. Means of the normalized percentages of the five monoterpenes in the 14 stands.

Population	18	19	20	21	22
1. Hinton	7.96%	11.27%	2.62%	20.79%	57.36%
2. Onoway	75.25	6.50	1.39	14.91	1.96
3. Devon	72.96	9.94	1.82	12.23	3.04
4. Cold Lake	75.67	10.76	0.01	13.22	0.34
5. Cypress Hills	5.92	9.89	0.19	15.60	68.40
6. Coleman	6.82	18.62	0.13	15.10	59.33
7. Canmore	8.57	17.90	0.11	10.52	62.90
8. Lake Abraham	7.52	22.97	0.00	13.76	55.74
9. Rocky Mt. House	14.32	16.26	0.00	23.28	46.14
10. Two Creeks	25.19	11.96	0.08	19.78	42.99
11. Peace River	83.20	10.01	0.82	3.04	2.92
12. Twin Lakes	26.67	12.82	0.01	18.26	42.24
13. Chinchaga River	81.88	10.14	0.00	4.79	3.19
14. Ft.Vermillion	81.66	14.92	0.14	3.25	0.03

Table 14. Factor score coefficients and communalities from principal component analysis of 22 variables for all stands.

	Factor Score Coefficients							
Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Communality
1	0.1218	0.0181	-0.0541	-0.0614	-0.0246	0.0545	0.0240	0.8636
2	-0.0386	0.0154	-0.1149	-0.4107	0.0167	0.0143	0.1277	0.5665
3	0.1193	0.0152	-0.0062	0.0883	-0.0230	0.0576	-0.0403	0.8309
4	0.1038	-0.0441	0.0799	0.0150	0.1235	-0.2164	0.3816	0.8831
5	-0.0750	0.0838	-0.2735	0.0609	0.2043	0.3096	0.0079	0.8306
6	-0.0615	-0.0866	-0.0618	0.0646	0.0328	0.2923	0.2231	0.4817
7	0.1230	0.0251	-0.0125	-0.0477	-0.0298	-0.0501	-0.0021	0.8713
8	-0.1156	-0.0225	0.1159	0.0064	0.0480	-0.0324	0.0241	0.8055
9	0.0401	-0.0185	0.3823	-0.3049	0.0440	0.2200	0.0693	0.8315
10	0.0800	0.1067	-0.0596	-0.3357	-0.0233	-0.0049	-0.1697	0.8246
11	-0.0115	0.2704	0.1303	0.0251	-0.0026	0.0915	-0.0155	0.9773
12	-0.0243	0.1457	0.1372	-0.1079	0.0683	-0.4315	0.3975	0.7721
13	-0.0420	-0.1275	0.3964	0.0651	0.0623	0.2043	0.2305	0.8933
14	-0.0297	0.2540	0.1525	0.1265	-0.0070	0.0882	0.0256	0.9697
15	-0.0221	0.2699	0.0530	0.0992	-0.0164	0.0505	-0.0334	0.9689
16	0.0448	0.0438	-0.2224	0.0987	0.4232	0.0853	0.5205	0.9358
17	0.0146	-0.0053	0.0579	0.3395	0.0197	-0.3528	-0.1712	0.4890
18	-0.1235	-0.0173	-0.0151	-0.0446	-0.0666	-0.1724	0.0689	0.9173
19	0.0188	0.0458	-0.0685	0.0579	-0.5054	0.3619	0.3090	0.8085
20	0.0819	-0.0369	0.1224	0.2491	-0.1098	0.1347	0.1030	0.6507
21	0.0418	0.0035	0.1399	0.0149	0.4441	0.2741	-0.3444	0.7441
22	0.1259	0.0112	-0.0438	0.0244	-0.0289	-0.0135	0.0189	0.9037
percentage variance	34.1	16.0	7.9	7.2	6.3	4.9	4.6	
cumulative percentage variance	34.1	50.1	58.0	65.2	71.5	76.4	81.0	

Table 15. Allocation of trees to the five groups obtained from 22 variable cluster analysis of all stands.

Stand	Trees in the stand allocated to: Group 1	Group 2	Group 3	Group 4	Group 5
Hinton	41 (100.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
Onoway	0 (0.0%)	5 (12.5%)	14 (35.0%)	16 (40.0%)	5 (12.5%)
Devon	0 (0.0%)	14 (25.9%)	7 (13.0%)	12 (22.2%)	21 (38.9%)
Cold Lake	0 (0.0%)	7 (16.3%)	32 (74.4%)	3 (7.0%)	1 (2.3%)
Total	41	26	53	31	27

Table 16. Means of the 22 variables for each of the five groups obtained from 22 variable cluster analysis of all stands.

Variable	Groups						Univariate
	1	2	3	4	5	Total	F
1	60.05	33.38	34.16	34.04	33.09	39.82	207.30
2	1.31	1.39	1.44	1.38	1.26	1.37	11.41
3	46.27	24.17	23.79	24.70	27.14	29.69	131.61
4	117.24	70.65	4.85	35.71	7.59	46.14	95.90
5	0.019	0.078	0.236	0.136	0.153	0.133	30.15
6	2.78	4.65	4.75	6.35	4.56	4.53	16.26
7	1.88	0.58	0.58	0.52	0.54	0.86	248.42
8	63.7	173.1	155.4	159.7	163.3	138.8	153.55
9	44.10	44.35	39.79	41.55	41.41	42.00	6.08
10	25.54	21.08	22.66	19.68	19.81	22.14	35.84
11	21.12	24.50	29.62	0.55	29.85	21.89	121.90
12	140.2	318.4	172.4	68.6	150.8	165.0	77.88
13	1.74	2.12	1.76	2.12	2.09	1.92	30.14
14	0.82	1.16	1.31	0.03	1.52	0.99	140.08
15	0.475	0.553	0.746	0.016	0.730	0.526	138.71
16	126.02	105.33	100.87	94.11	74.44	102.13	9.59
17	3.50	2.31	1.65	2.59	4.34	2.74	3.99
18	8.83	77.05	77.14	74.15	65.49	59.10	216.60
19	11.43	7.86	9.70	7.51	11.32	9.69	3.81
20	2.51	1.17	0.55	1.34	2.01	1.45	44.33
21	20.70	12.93	11.61	14.64	17.64	15.34	3.69
22	56.54	0.99	1.00	2.36	3.54	14.41	440.08
Group Members	41	26	53	31	27	178	

Table 17. Discriminant function coefficients for the five groups obtained from 22 variable cluster analysis of all stands.

Variable	Standardized Coefficients			
	Function 1	Function 2	Function 3	Function 4
1	0.2298	0.0066	0.0363	0.0076
2	-0.0308	-0.0320	-0.0764	0.3005
4	0.1076	0.1111	0.5277	0.1956
6	-0.0321	-0.1143	0.0202	0.0332
7	0.1678	-0.0059	-0.1013	0.2313
8	-0.0988	0.0435	0.0847	0.0157
12	0.0133	0.1712	0.7612	0.2834
13	-0.0522	-0.1936	0.1764	0.1131
14	0.0968	1.1868	0.6491	-2.0324
15	-0.0420	-0.3334	-1.0185	1.9315
16	-0.0138	-0.1094	-0.0593	0.2240
17	0.0279	-0.0303	0.0396	-0.2304
18	-0.2435	1.4069	-1.7684	13.5222
19	0.0161	0.2989	-0.3263	2.3343
21	-0.0565	0.5540	-0.7502	5.4425
22	0.2248	1.1325	-1.4999	10.6987
Relative Percentage	75.55	13.07	7.80	3.58

Table 18. Predicted group membership based upon discriminant analysis of the five groups obtained from 22 variable cluster analysis of all stands.

Actual Group	No. Cases	Predicted Group Membership Group 1	Group 2	Group 3	Group 4	Group 5
1	41	41 (100.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
2	26	0 (0.0%)	24 (92.3%)	2 (7.7%)	0 (0.0%)	0 (0.0%)
3	53	0 (0.0%)	0 (0.0%)	53 (100.0%)	0 (0.0%)	0 (0.0%)
4	31	0 (0.0%)	1 (3.2%)	0 (0.0%)	30 (96.8%)	0 (0.0%)
5	27	0 (0.0%)	0 (0.0%)	1 (3.7%)	0 (0.0%)	26 (96.3%)

The percentage of grouped cases correctly classified was 97.75%.

Table 19. Factor score coefficients and communalities from principal component analysis of 5 variables for all stands.

Variable	Factor Score Coefficients		Communality
	Factor 1	Factor 2	
18	-0.3799	0.0891	0.9606
19	0.0925	0.6316	0.7143
20	0.2918	0.2249	0.6424
21	0.1717	-0.5663	0.7226
22	0.3504	0.0201	0.8070
Percentage Variance	51.3	25.7	
Cumulative Percentage Variance	51.3	76.9	

Table 20. Allocation of trees to the four groups obtained from 5 variable cluster analysis of all stands.

Stand	Trees in the stand allocated to: Group 1	Group 2	Group 3	Group 4
Hinton	45 (62.5%)	26 (36.1%)	1 (1.4%)	0 (0.0%)
Onoway	0 (0.0%)	0 (0.0%)	21 (40.4%)	31 (59.6%)
Devon	1 (1.4%)	3 (4.4%)	34 (49.3%)	31 (44.9%)
Cold Lake	0 (0.0%)	0 (0.0%)	35 (54.7%)	29 (45.3%)
Total	46	29	91	91

Table 21. Means of the 5 variables for each of the four groups obtained from 5 variable cluster analysis of all stands.

Variable	Groups					Univariate
	1	2	3	4	Total	F
18	7.33	13.23	83.40	66.52	55.89	702.36
19	6.89	18.34	11.24	7.17	9.82	53.35
20	2.12	3.53	0.94	1.11	1.51	69.51
21	26.15	11.72	2.60	23.98	15.42	145.66
22	57.51	53.18	1.82	1.22	17.37	694.31
Group Members	46	29	91	91	257	

Table 22. Discriminant function coefficients for the four groups obtained from 5 variable cluster analysis of all stands.

Variable	Standardized Coefficients		
	Function 1	Function 2	Function 3
18	-0.1022	2.5266	-2.8689
20	0.0868	-0.0608	0.6274
21	0.2053	1.7661	-0.6114
22	0.7899	1.8595	-3.0445
Relative Percentage	82.49	15.72	1.79

Table 23. Predicted group membership based upon discriminant analysis of the four groups obtained from 5 variable cluster analysis of all stands.

Actual Group	No. Cases	Predicted Group Membership Group 1	Group 2	Group 3	Group 4
1	46	44 (95.7%)	0 (0.0%)	0 (0.0%)	2 (4.3%)
2	29	1 (3.4%)	25 (86.2%)	2 (6.9%)	1 (3.4%)
3	91	0 (0.0%)	0 (0.0%)	88 (96.7%)	3 (3.3%)
4	91	0 (0.0%)	0 (0.0%)	5 (5.5%)	86 (94.5%)

The percentage of grouped cases correctly classified was 94.55%.

Table 24. Factor score coefficients and communalities from principal component analysis of 22 variables for the putative hybrid stands.

	Factor Score Coefficients									
Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	Factor 6	Factor 7	Factor 8	Factor 9	Communality
1	-0.0259	-0.0303	0.3036	-0.0601	-0.0649	0.0975	0.0419	0.1908	0.0376	0.6545
2	-0.0708	-0.0705	0.0102	0.1359	0.3807	0.2726	0.1547	-0.0821	-0.0739	0.8546
3	0.0383	0.0445	0.2332	-0.1376	-0.3641	-0.1824	-0.0975	0.1899	0.0889	0.9522
4	-0.1076	-0.0423	0.0182	0.3391	-0.0192	-0.0383	-0.2358	0.4054	0.0706	0.9473
5	0.1147	-0.0972	0.0211	-0.1885	0.1887	-0.2182	0.3482	-0.1286	0.3339	0.9676
6	-0.1022	-0.0243	-0.0528	-0.0043	-0.1170	-0.1691	0.2923	0.1927	-0.1637	0.4964
7	-0.0042	0.1070	0.1809	-0.0433	0.2144	0.1158	-0.4205	-0.0119	0.0772	0.7279
8	0.0207	-0.0421	-0.1170	0.2185	-0.1574	-0.0817	0.1441	-0.1492	-0.3098	0.5397
9	-0.0633	0.1039	0.2135	0.1598	-0.1371	0.2087	0.2475	-0.2228	0.2500	0.9026
10	0.0702	-0.0704	0.2790	-0.0511	0.0782	0.0886	0.1162	0.0356	-0.2558	0.7094
11	0.2381	0.0559	0.0394	0.1037	-0.0411	0.0661	0.0370	-0.0217	0.0285	0.9580
12	0.1355	-0.0789	0.0005	0.2710	0.0384	0.0832	-0.0620	0.2023	0.0009	0.6991
13	-0.1164	0.1499	-0.0192	0.1881	-0.1882	0.1200	0.1530	-0.2278	0.4335	0.9733
14	0.2333	0.0704	-0.0219	0.1164	-0.0514	0.0551	0.0150	-0.0368	0.0681	0.9460
15	0.2437	0.0346	-0.0138	0.0697	-0.0248	0.0301	-0.0175	-0.0094	-0.0013	0.9374
16	0.0128	-0.1498	0.0417	0.1647	0.1872	-0.2863	0.1351	0.2990	0.4369	0.9602
17	0.0191	0.0115	-0.1787	-0.0545	-0.0159	-0.0927	-0.3806	-0.1813	0.3211	0.5997
18	0.0120	-0.2825	-0.0600	-0.0752	-0.1710	0.2539	-0.0468	0.0265	0.1074	0.9629
19	0.0276	0.1582	-0.1675	-0.0898	-0.0518	0.1786	0.1822	0.3531	0.0392	0.7093
20	0.0217	0.2634	-0.0875	-0.0011	0.0507	-0.0021	0.1080	0.2804	-0.1018	0.7545
21	-0.0192	0.1737	0.1346	0.1646	0.1337	-0.3637	-0.0349	-0.2336	-0.1778	0.9600
22	-0.0119	0.1894	-0.0290	-0.1574	0.1904	0.0919	0.0572	0.2164	0.1610	0.6132
percentage variance	17.7	13.0	11.0	9.0	7.6	7.3	5.6	5.1	4.8	
cumulative percentage variance	17.7	30.7	41.7	50.7	58.3	65.6	71.2	76.3	81.0	

Table 25. Allocation of trees to the four groups obtained from 22 variable cluster analysis of the putative hybrid stands.

Stand	Trees in the stand allocated to: Group 1	Group 2	Group 3	Group 4
Onoway	11 (27.5%)	14 (35.0%)	11 (27.5%)	4 (10.0%)
Devon	22 (40.7%)	11 (20.4%)	17 (31.5%)	4 (7.4%)
Total	33	25	28	8

Table 26. Means of the 22 variables for each of the four groups obtained from 22 variable cluster analysis of the putative hybrid stands.

Variable	Groups					Univariate
	1	2	3	4	Total	F
1	33.78	33.92	33.04	37.29	33.89	2.23
2	1.36	1.39	1.30	1.28	1.34	2.78
3	24.83	24.47	25.48	32.35	25.57	5.05
4	23.79	41.60	34.07	34.00	32.46	0.82
5	0.198	0.131	0.119	0.108	0.149	3.61
6	4.52	6.36	5.25	3.50	5.14	5.46
7	0.50	0.50	0.50	0.94	0.54	192.14
8	166.4	160.2	170.4	140.6	163.7	4.32
9	43.12	42.20	37.86	44.50	41.42	6.90
10	20.42	19.76	20.57	22.25	20.45	2.22
11	29.24	0.00	25.14	24.12	19.81	117.75
12	205.0	53.6	217.8	134.5	162.6	22.07
13	2.12	2.15	1.86	2.02	2.04	6.62
14	1.44	0.00	1.23	1.07	0.96	124.03
15	0.688	0.000	0.664	0.548	0.486	105.41
16	106.59	97.70	85.92	81.73	95.95	1.87
17	3.32	2.85	2.97	3.21	3.08	0.09
18	65.95	73.49	84.63	60.46	73.05	18.63
19	8.37	7.64	9.13	6.58	8.25	1.02
20	1.89	1.49	1.44	1.82	1.64	3.18
21	21.27	14.64	3.63	25.11	14.58	18.40
22	2.52	2.74	1.16	6.04	2.47	2.84
Group Members	33	25	28	8	94	

Table 27. Discriminant function coefficients for the four groups obtained from 22 variable cluster analysis of the putative hybrid stands.

Variable	Standardized Coefficients		
	Function 1	Function 2	Function 3
1	0.3983	0.3234	0.1257
2	-0.3150	-0.4536	0.2484
3	-0.7135	-0.4442	-0.0552
4	-0.0051	0.1624	-0.4154
6	0.0020	0.0097	-0.1813
7	-0.9405	-0.0019	-0.1992
11	-0.0089	-0.0620	1.4099
12	0.0048	0.3497	-0.0761
13	0.0027	-0.0289	0.3352
15	-0.0066	0.8346	-1.1701
16	-0.0042	-0.1969	0.4755
17	-0.0029	-0.0550	0.2381
20	-0.0045	-0.0252	0.2381
21	0.0030	-0.0771	0.5386
Relative Percentage	99.37	0.45	0.18

Table 28. Predicted group membership based upon discriminant analysis of the four groups obtained from 22 variable cluster analysis of the putative hybrid stands.

Actual Group	No. Cases	Predicted Group Membership			
		Group 1	Group 2	Group 3	Group 4
1	33	33 (100.0%	0 (0.0%)	0 (0.0%)	0 (0.0%)
2	25	0 (0.0%)	25 (100.0%)	0 (0.0%)	0 (0.0%)
3	28	0 (0.0%)	1 (3.6%)	27 (96.4%)	0 (0.0%)
4	8	0 (0.0%)	0 (0.0%)	0 (0.0%)	8 (100.0%)

The percentage of grouped cases correctly classified was 98.94%.

Table 29. Factor score coefficients and communalities from principal component analysis of 5 variables for the putative hybrid stands.

Variable	Factor Score Coefficients		Communality
	Factor 1	Factor 2	
18	-0.4124	0.2119	0.9649
19	0.1566	0.4385	0.5896
20	0.3460	0.2372	0.7389
21	0.2733	-0.5025	0.9880
22	0.2382	0.3103	0.5192
Percentage Variance	44.9	31.1	
Cumulative Percentage Variance	44.9	76.0	

Table 30. Allocation of trees to the four groups obtained from 5 variable cluster analysis of the putative hybrid stands.

Stand	Trees in the stand allocated to: Group 1	Group 2	Group 3	Group 4
Onoway	28 (53.8%)	20 (38.5%)	2 (3.8%)	2 (3.8%)
Devon	24 (34.8%)	16 (23.2%)	8 (11.6%)	21 (30.4%)
Total	52	36	10	23

Table 31. Means of the 5 variables for each of the four groups obtained from 5 variable cluster analysis of the putative hybrid stands.

Variable	Groups					Univariate
	1	2	3	4	Total	F
18	64.59	88.76	58.86	78.45	73.94	97.64
19	6.94	6.28	11.56	13.98	8.46	34.42
20	1.67	1.09	2.80	1.90	1.64	46.83
21	25.51	2.96	10.60	3.50	13.38	101.00
22	1.29	0.91	16.20	2.16	2.57	126.41
Group Members	52	36	10	23	121	

Table 32. Discriminant function coefficients for the four groups obtained from 5 variable cluster analysis of the putative hybrid stands.

Variable	Standardized Coefficients		
	Function 1	Function 2	Function 3
19	-0.1439	0.1524	-0.8454
20	-0.3312	-0.0263	-0.2679
21	-0.1252	-0.9450	-0.2099
22	-0.7498	-0.0237	0.5975
Relative Percentage	62.57	30.67	6.77

Table 33. Predicted group membership based upon discriminant analysis of the four groups obtained from 5 variable cluster analysis of the putative hybrid stands.

Actual Group	No. Cases	Predicted Group Membership			
		Group 1	Group 2	Group 3	Group 4
1	52	52 (100.0%)	0 (0.0%)	0 (0.0%)	0 (0.0%)
2	36	1 (2.8%)	35 (97.2%)	0 (0.0%)	0 (0.0%)
3	10	1 (10.0%)	0 (0.0%)	9 (90.0%)	0 (0.0%)
4	23	0 (0.0%)	0 (0.0%)	1 (4.3%)	22 (95.7%)

The percentage of grouped cases correctly classified was 97.52%.

Table 34. Discriminant function coefficients for the Hinton/Cold Lake classification of the 14 study stands.

Variable	Standardized Coefficients
	Function 1
18	-4.9877
19	-0.8644
21	-1.6682
22	-3.4210
Relative Percentage	100.00

Table 35. Classification of individuals in the 14 stands by discriminant analysis.

Population	No. of Individuals	Number classified as: Pinus contorta	P. banksiana	Percentage P. banksiana
1. Hinton	72	70	2	2.8%
2. Onoway	52	0	52	100.0%
3. Devon	69	1	68	98.6%
4. Cold Lake	64	0	64	100.0%
5. Cypress Hills	39	39	0	0.0%
6. Coleman	35	34	1	2.9%
7. Canmore	25	24	1	4.0%
8. Lake Abraham	38	37	1	2.6%
9. Rocky Mt. House	34	27	7	20.6%
10. Two Creeks	32	20	12	37.5%
11. Peace River	32	0	32	100.0%
12. Twin Lakes	38	22	16	42.1%
13. Chinchaga River	28	0	28	100.0%
14. Ft. Vermillion	34	0	34	100.0%

Table 36. Hypothetical monoterpene compositions of F_1 hybrids and backcrosses with the Hinton and Cold Lake stands as parental populations, assuming independent assortment and no dominance effects.

	Normalized Monoterpene Percentages				
Population	α-pinene	β-pinene	myrcene	3-carene	β-phellandrene
Hinton (actual)	7.96%	11.27%	2.62%	20.79%	57.36%
Backcross to Hinton	24.89%	11.14%	1.97%	18.90%	43.11%
F_1	41.82%	11.02%	1.32%	17.00%	28.85%
Backcross to Cold Lake	58.75%	10.89%	0.67%	15.11%	14.60%
Cold Lake (actual)	75.67%	10.76%	0.01%	13.22%	0.34%

VIII. FIGURES

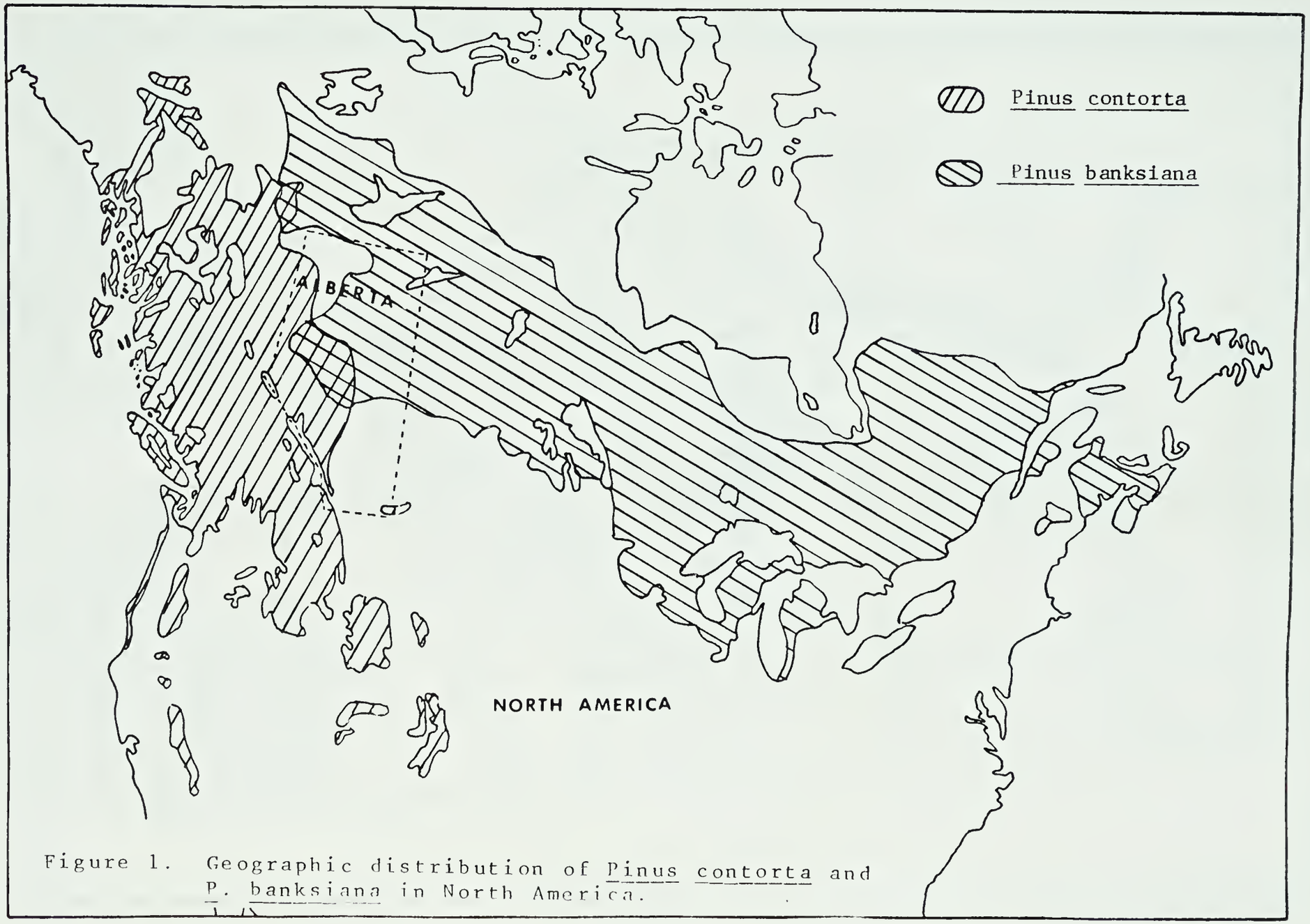

Figure 1. Geographic distribution of Pinus contorta and P. banksiana in North America.

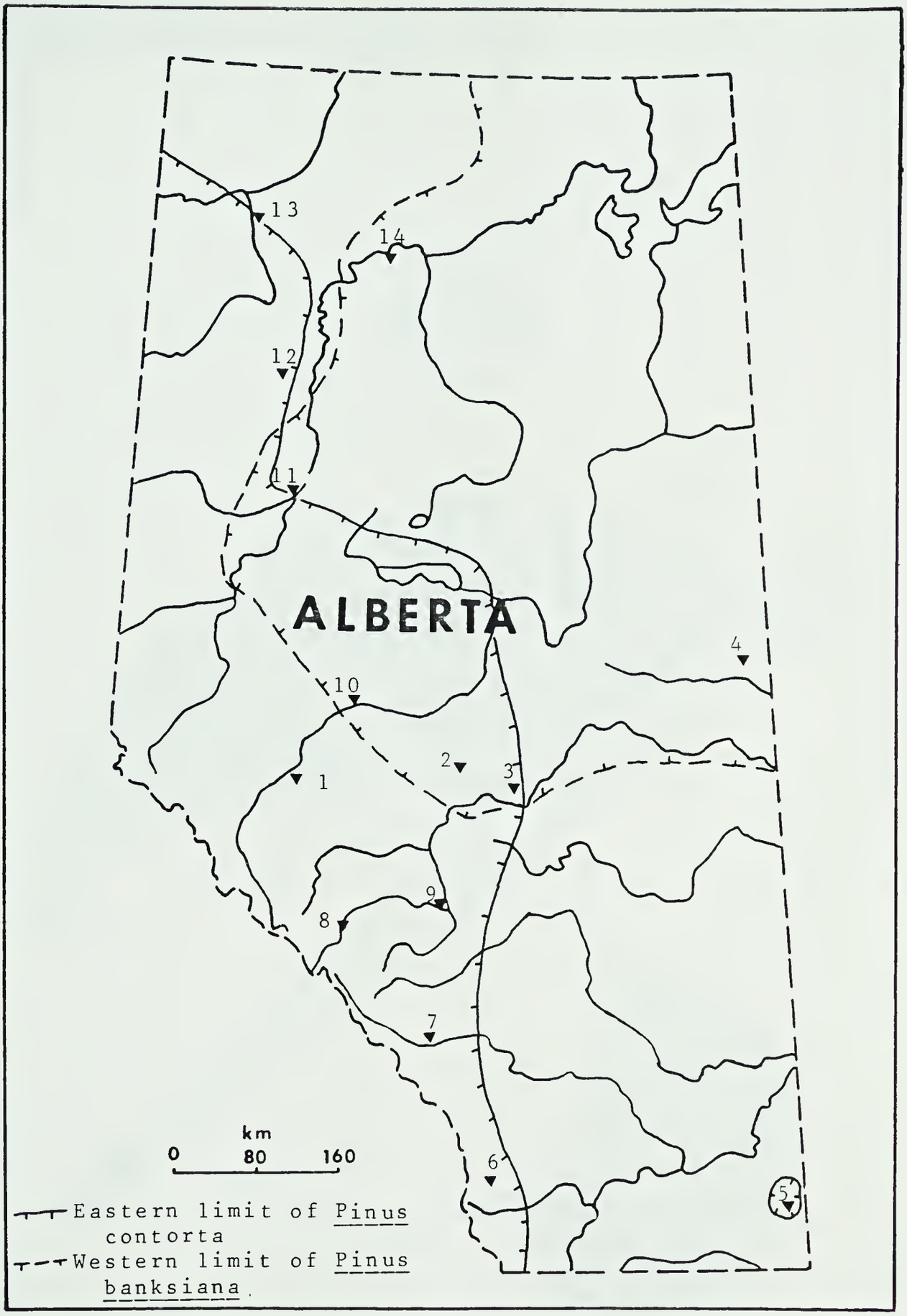

Figure 2. Geographic distribution of Pinus contorta and P. banksiana in Alberta, with study site locations.

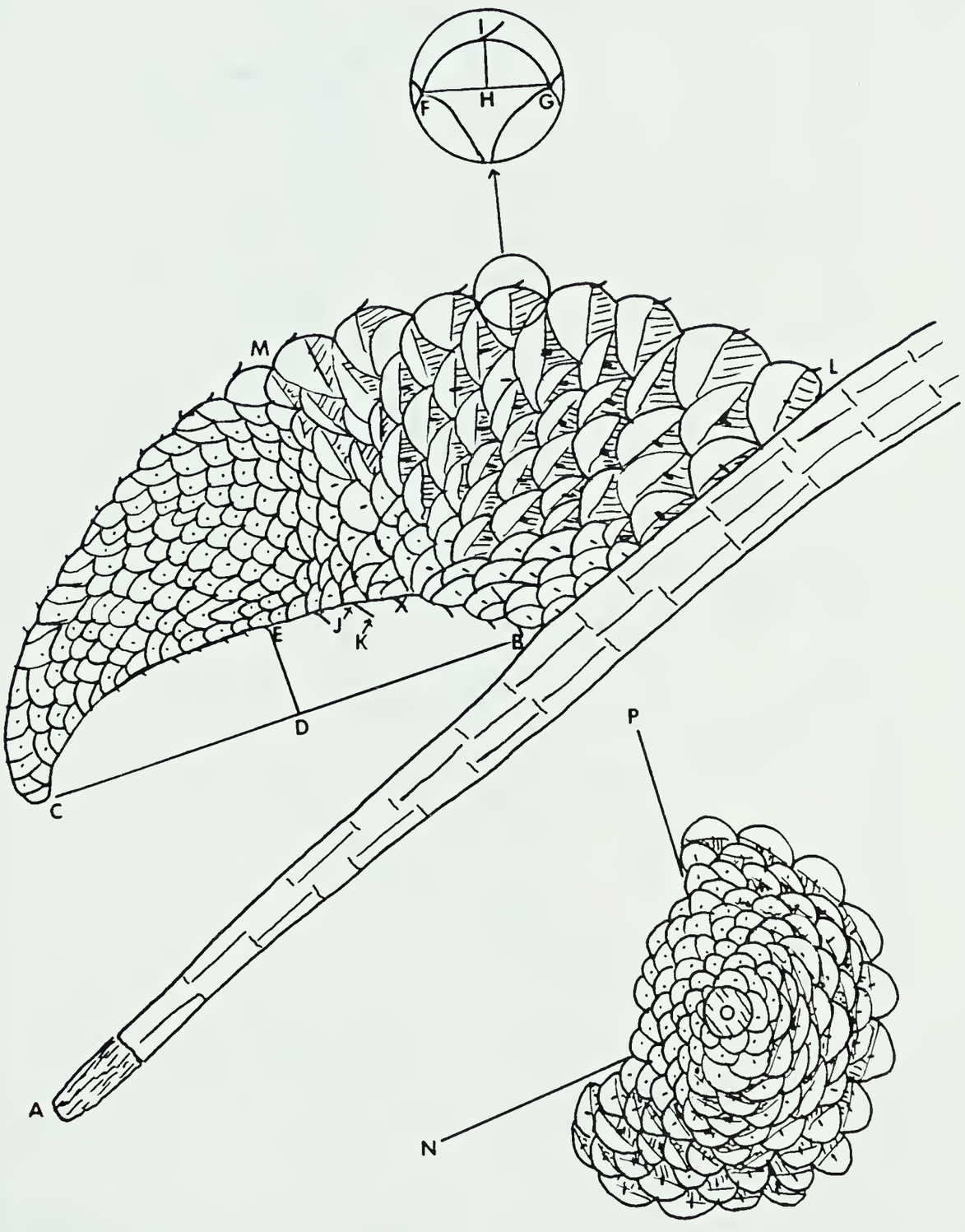

Figure 3. Illustration of a pine cone showing the variable measurements.

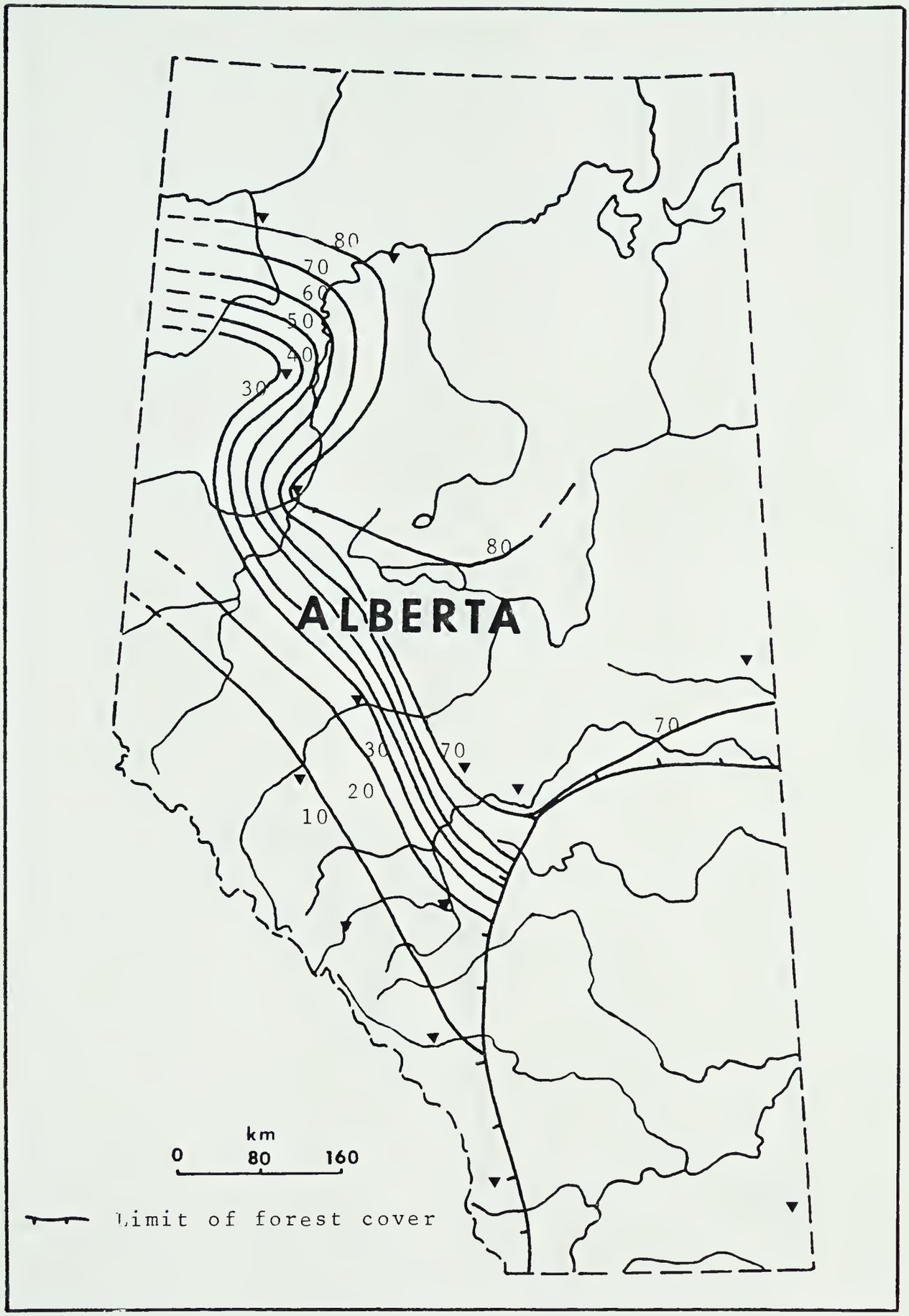

Figure 4. Isoconcentrations of -pinene (normalized percentage) in pine stands in Alberta

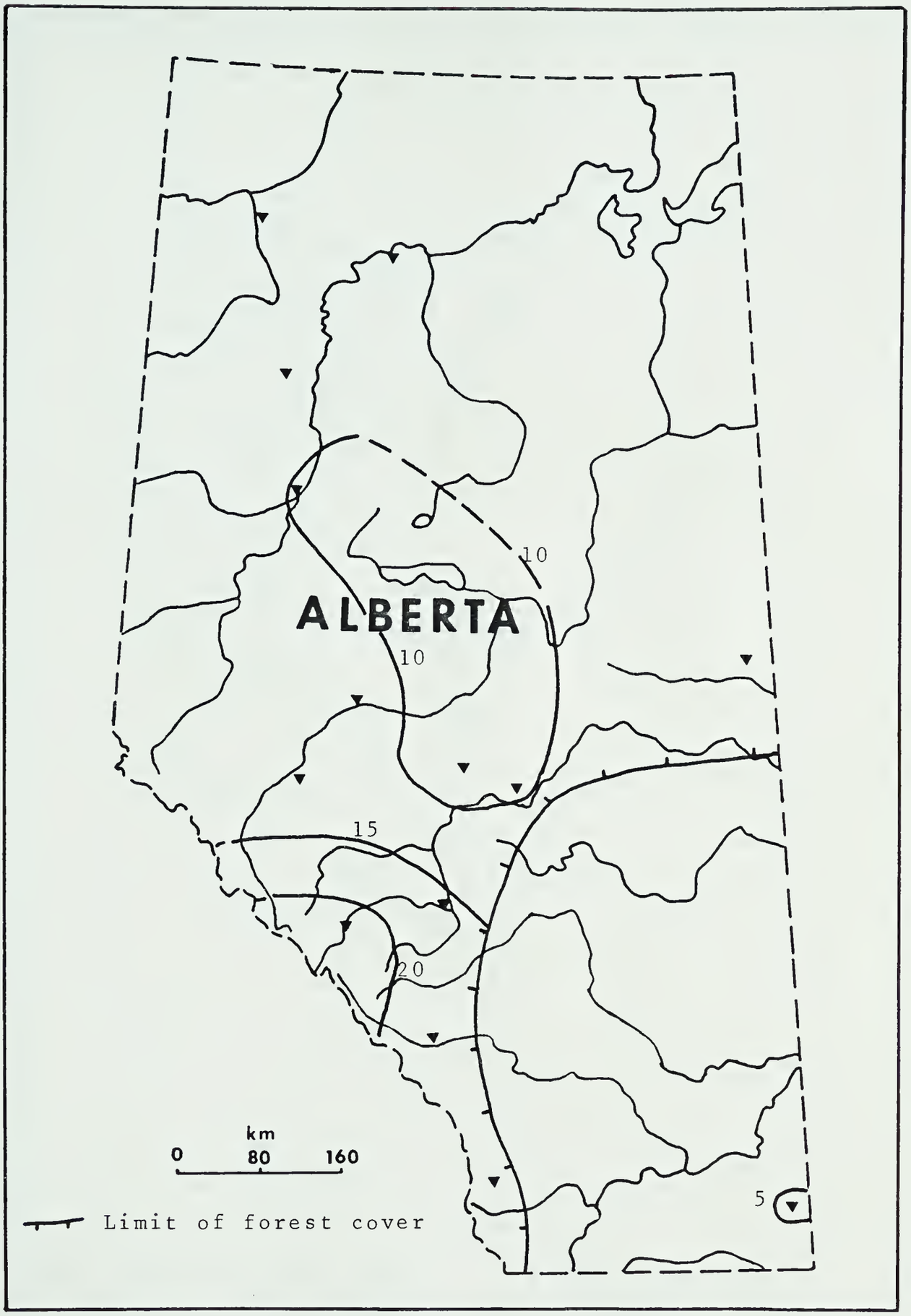

Figure 5. Isoconcentrations of -pinene (normalized percentage) in pine stands in Alberta.

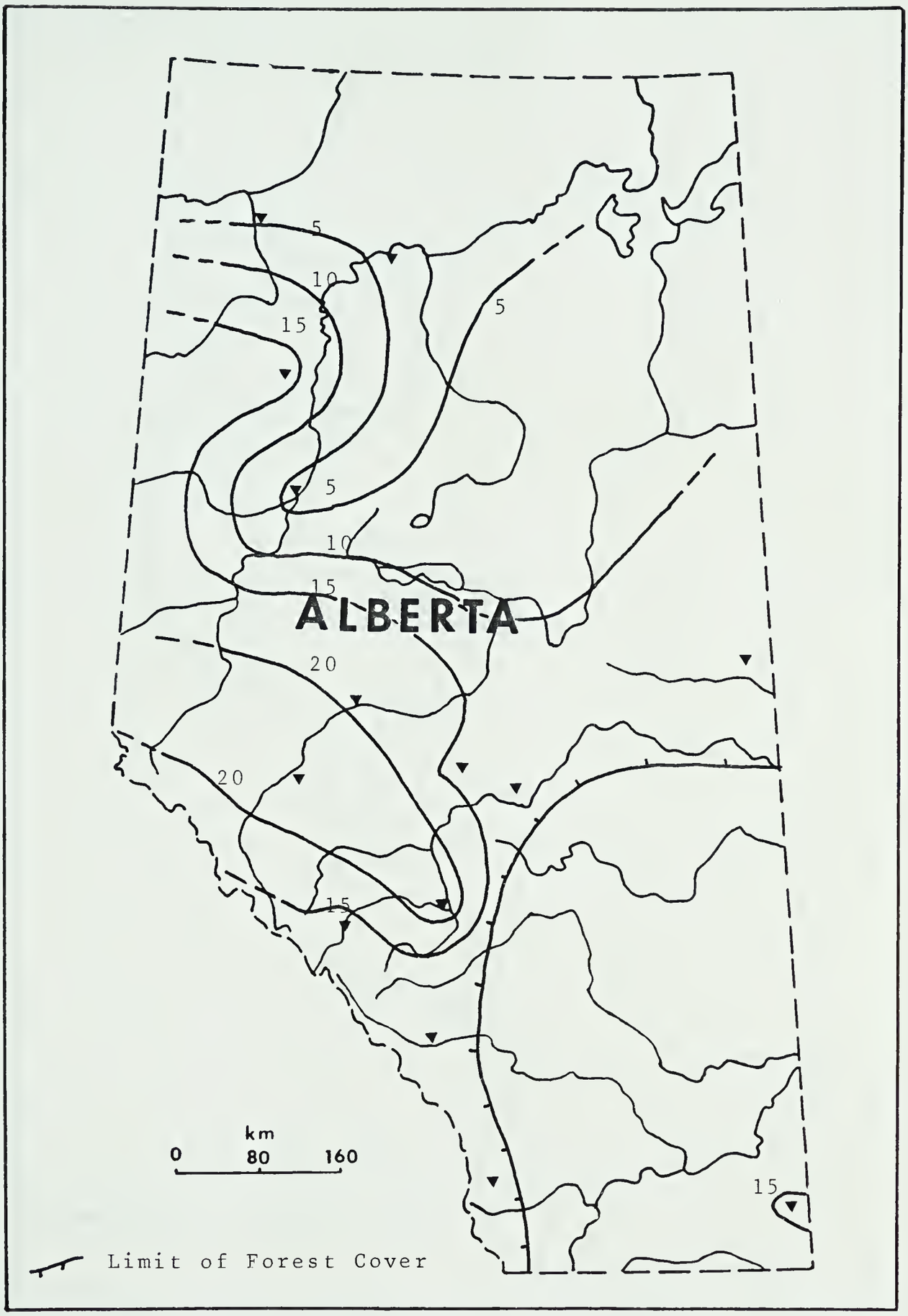

Figure 6. Isoconcentrations of 3-carene (normalized percentage) in pine stands in Alberta.

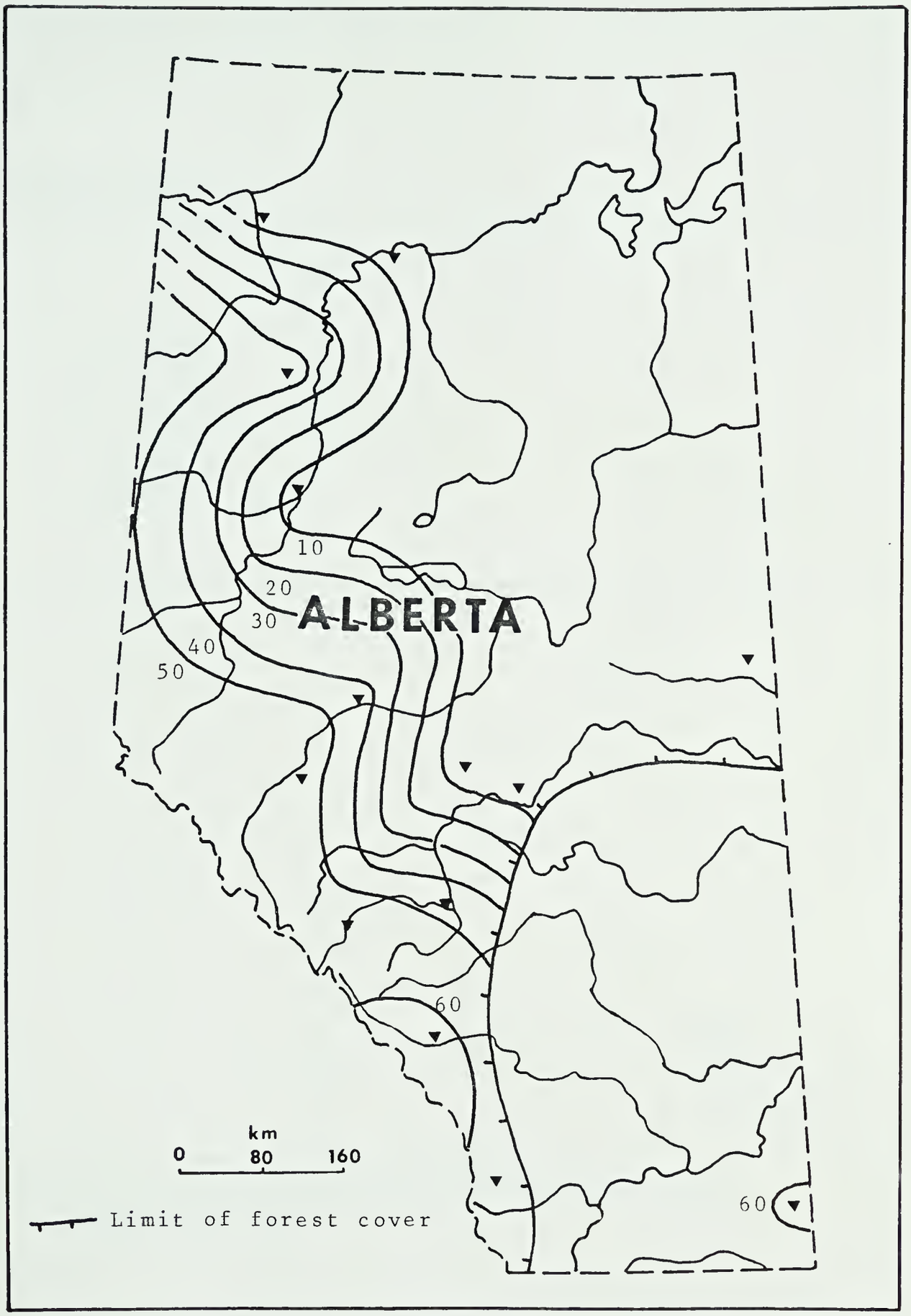

Figure 7. Isoconcentrations of -phellandrene (normalized percentage) in pine stands in Alberta.

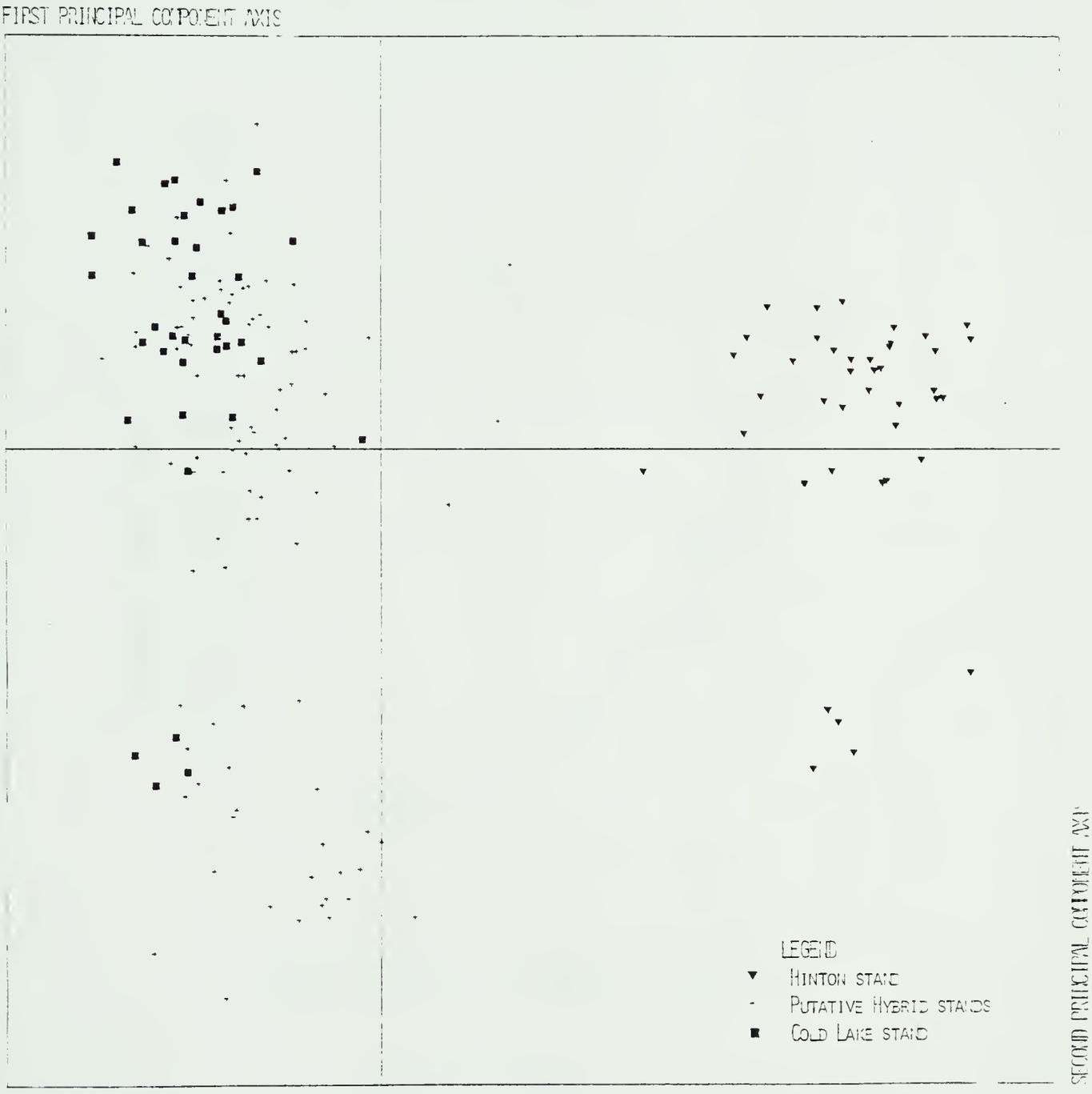

FIGURE 8. PLOT OF INDIVIDUALS FROM THE FOUR POPULATION STUDY STANDS, BASED ON 22 VARIABLE PRINCIPAL COMPONENT ANALYSIS.

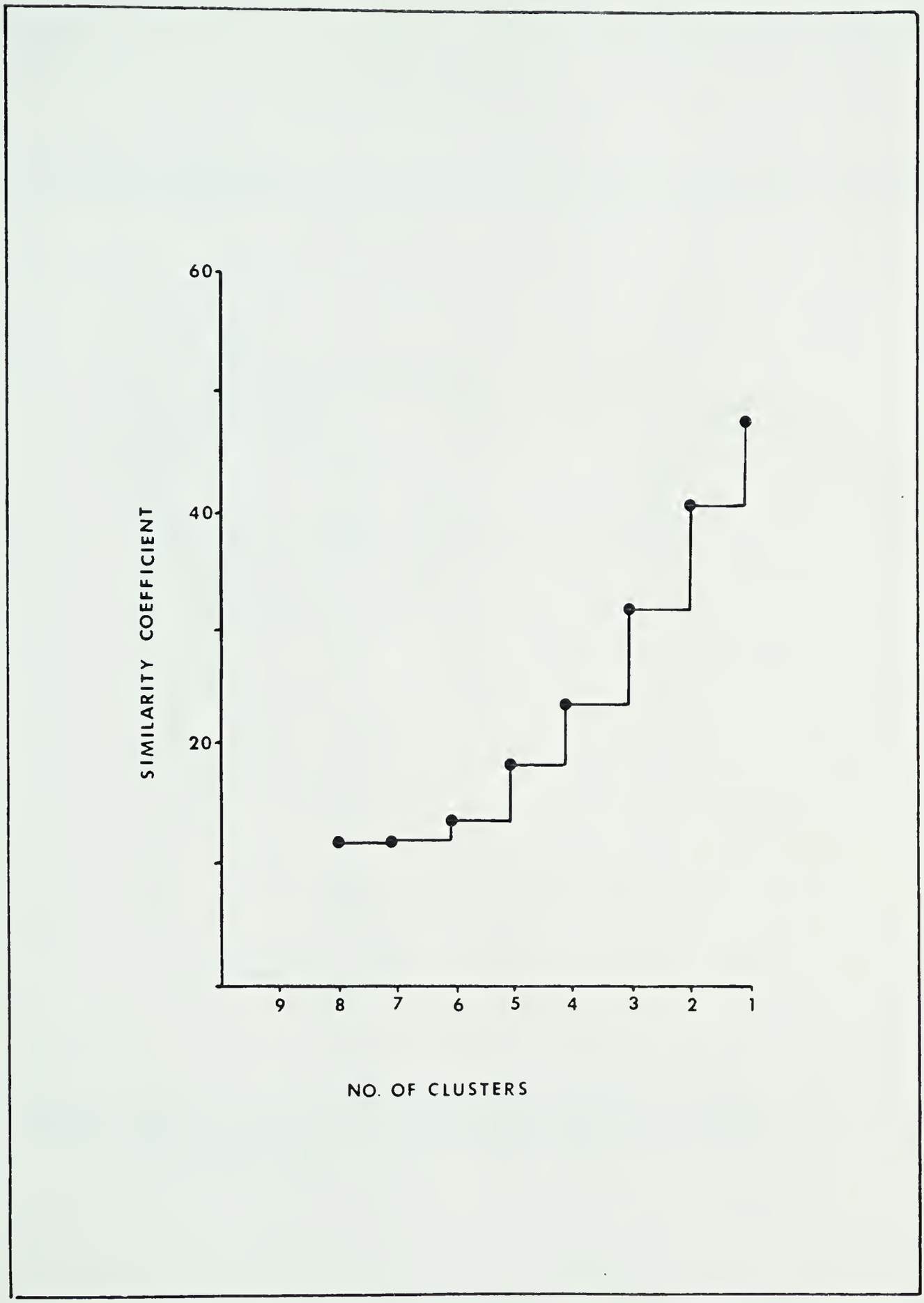

Figure 9. Similarity coefficients in 22 variable cluster analysis of all stands.

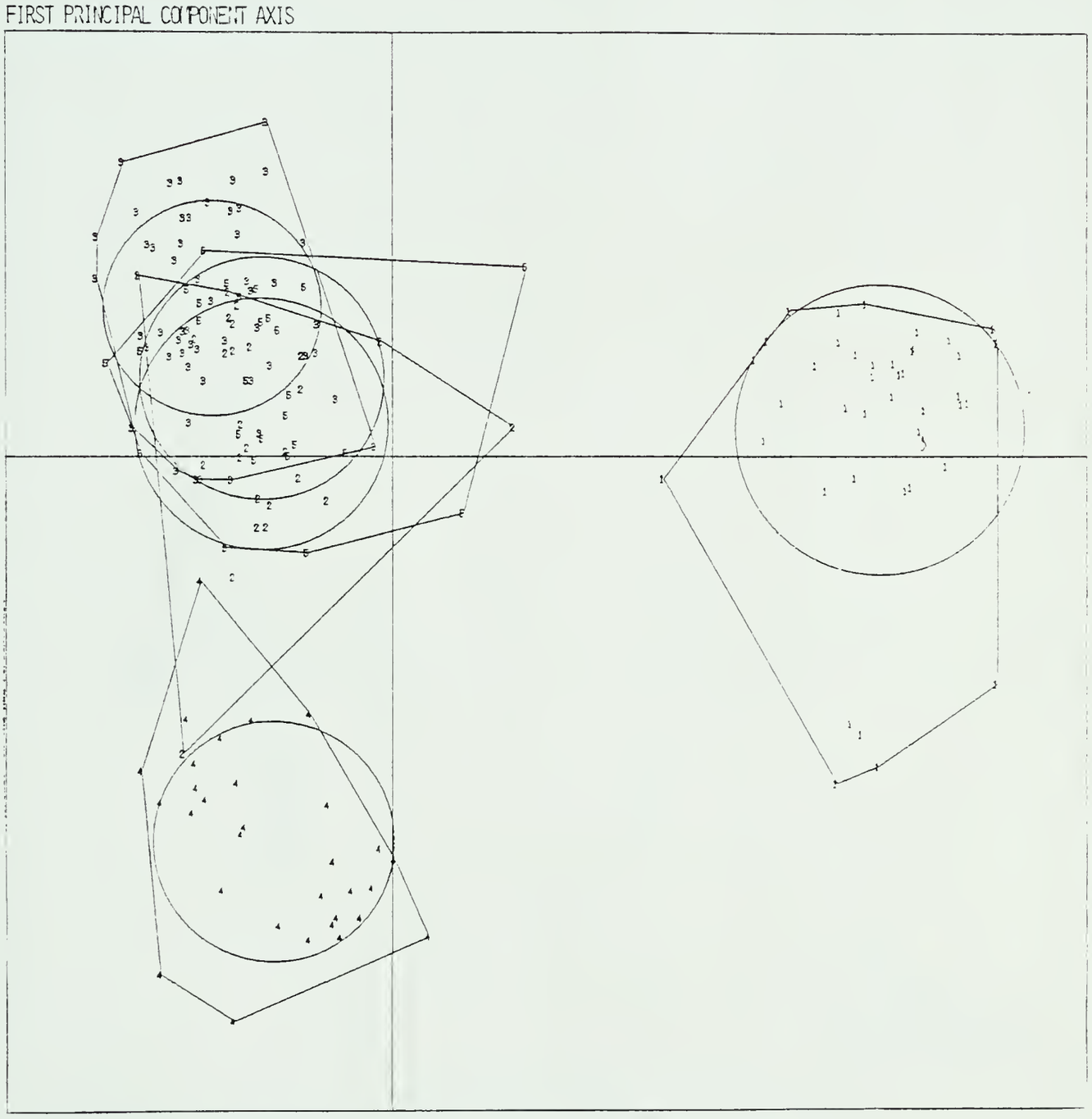

FIGURE 10. PLOT OF THE FIVE GROUPS OBTAINED FROM 22 VARIABLE CLUSTER ANALYSIS OF THE FOUR POPULATION STUDY STANDS.

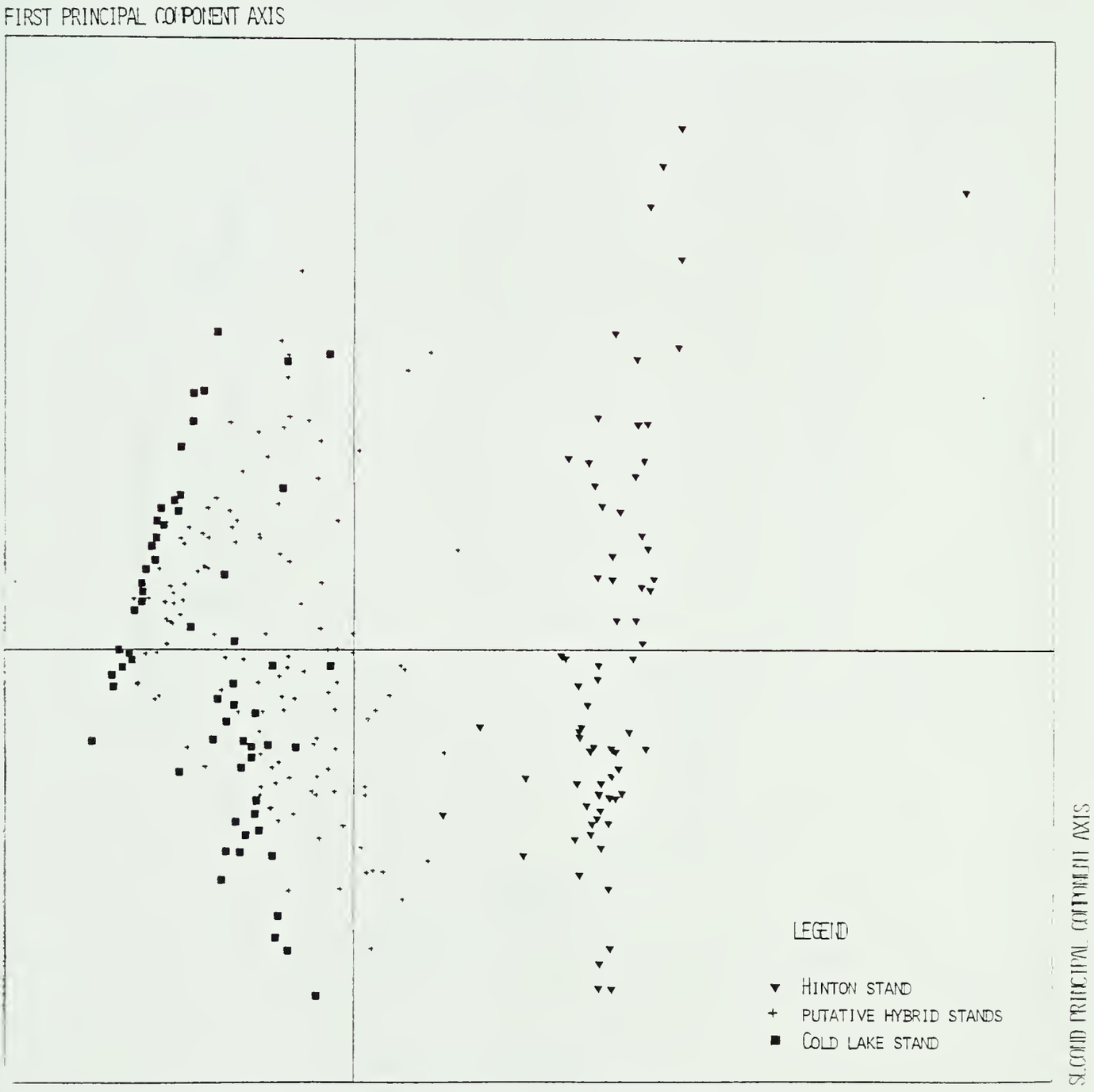

FIGURE 11. PLOT OF INDIVIDUALS FROM THE FOUR POPULATION STUDY STANDS, BASED ON 5 VARIABLE PRINCIPAL COMPONENT ANALYSIS.

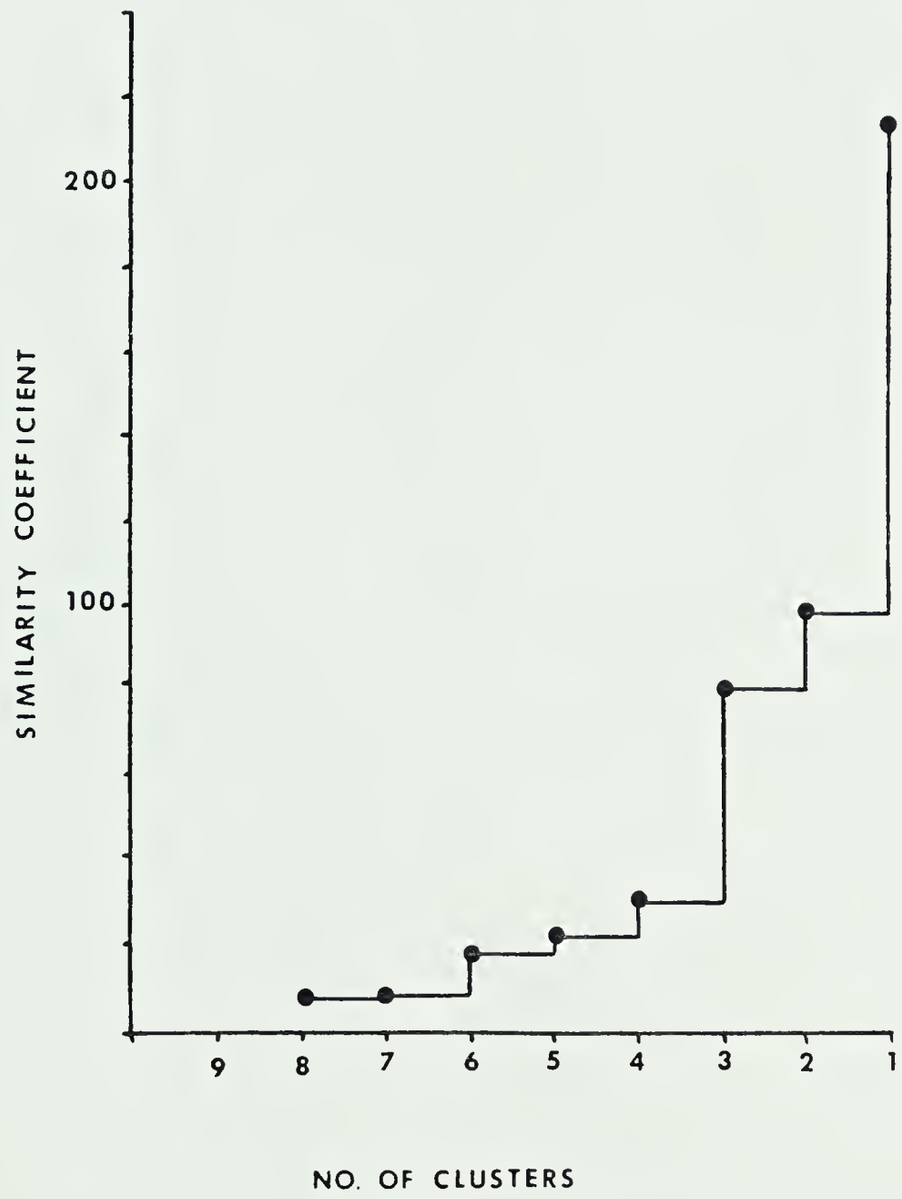

Figure 12. Similarity coefficients in 5 variable cluster analysis of all stands.

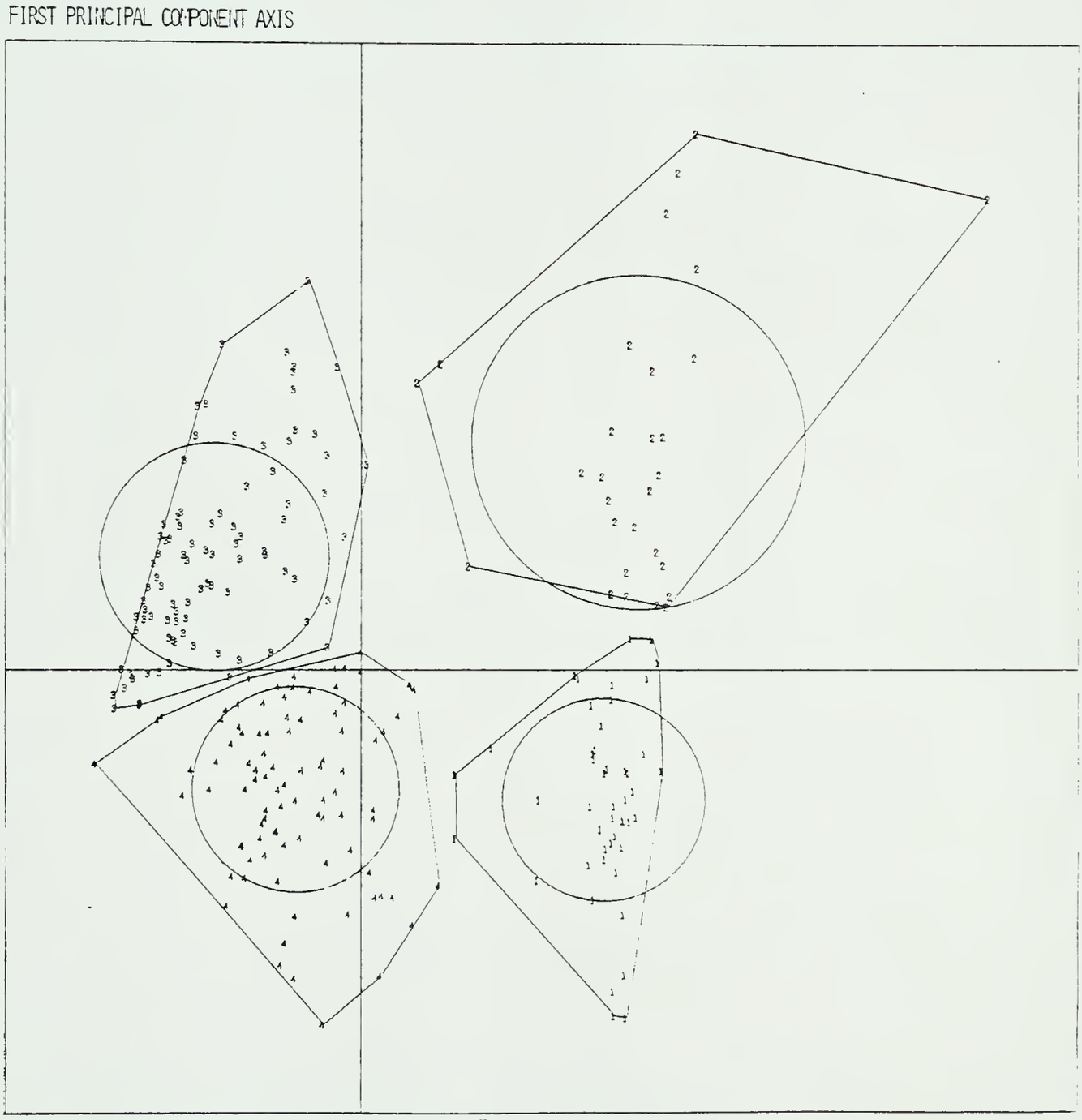

FIGURE 13. PLOT OF THE FOUR GROUPS OBTAINED FROM 5 VARIABLE CLUSTER ANALYSIS OF THE FOUR POPULATION STUDY STANDS.

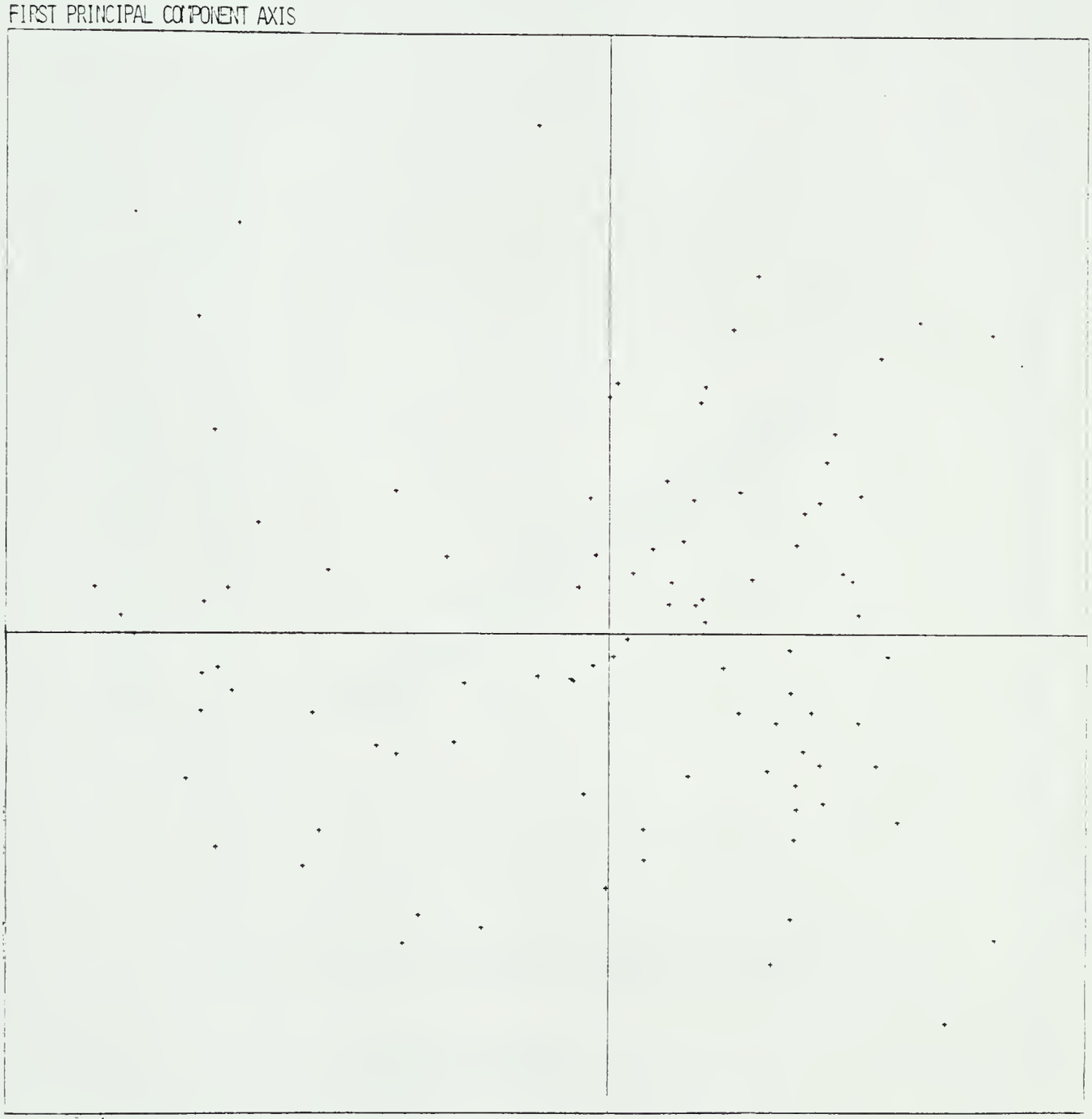

FIGURE 14. PLOT OF INDIVIDUALS FROM THE TWO PUTATIVE HYBRID STANDS, BASED ON 22 VARIABLE PRINCIPAL COMPONENT ANALYSIS.

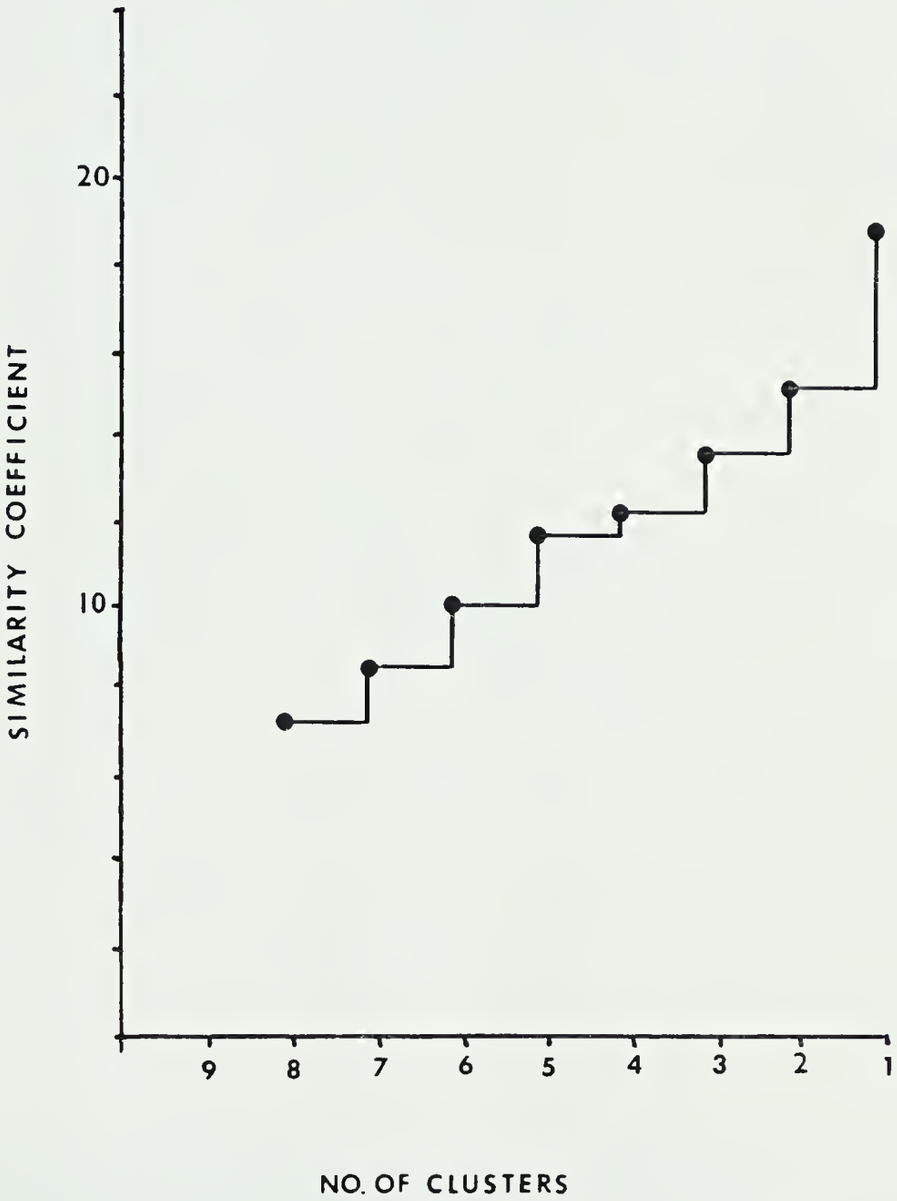

Figure 15. Similarity coefficients in 22 variable cluster analysis of the putative hybrid stands.

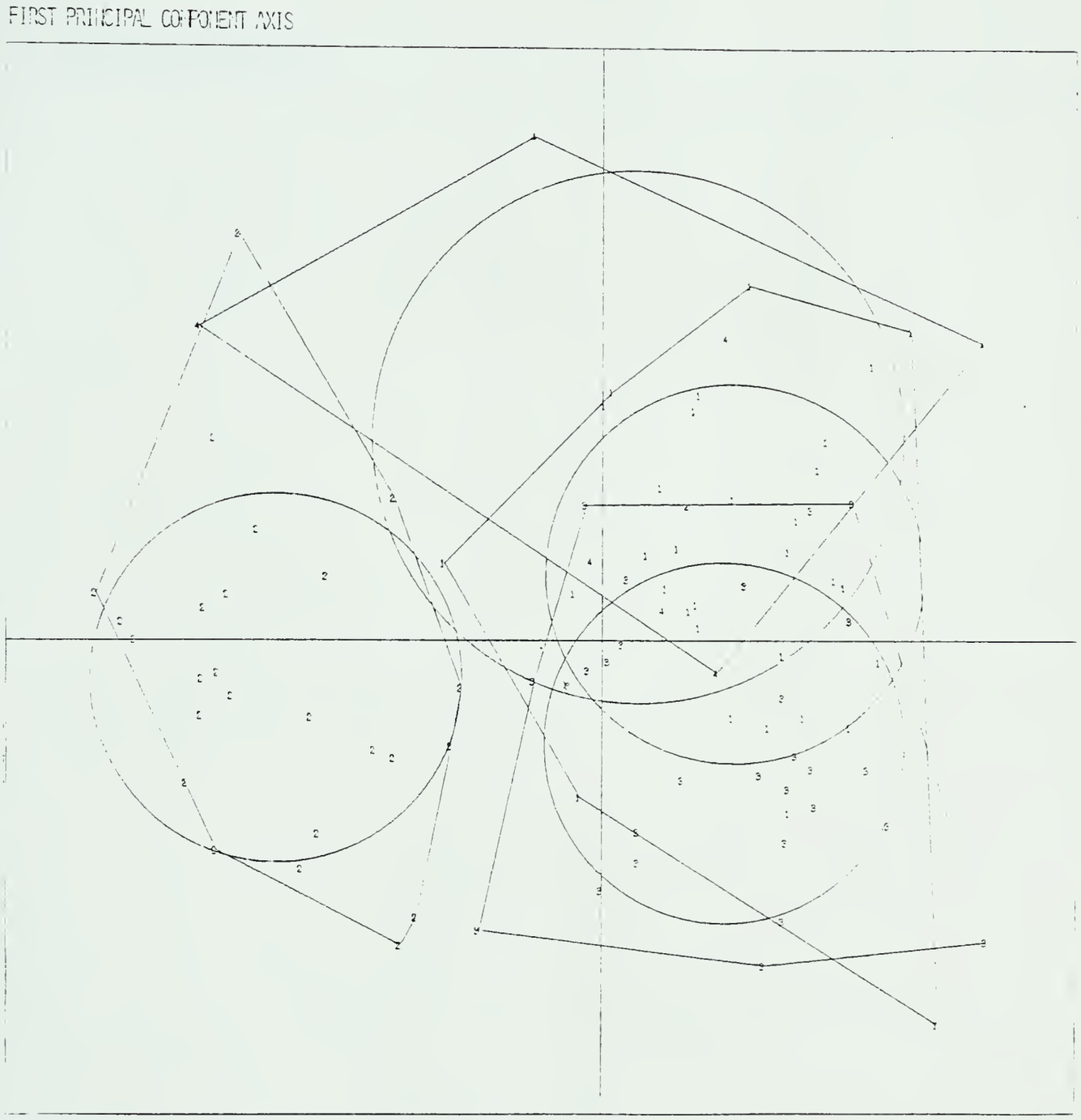

FIGURE 18. PLOT OF THE FOUR GROUPS OBTAINED FROM 22 VARIABLE CLUSTER ANALYSIS OF THE TWO PUTATIVE HYBRID STANDS.

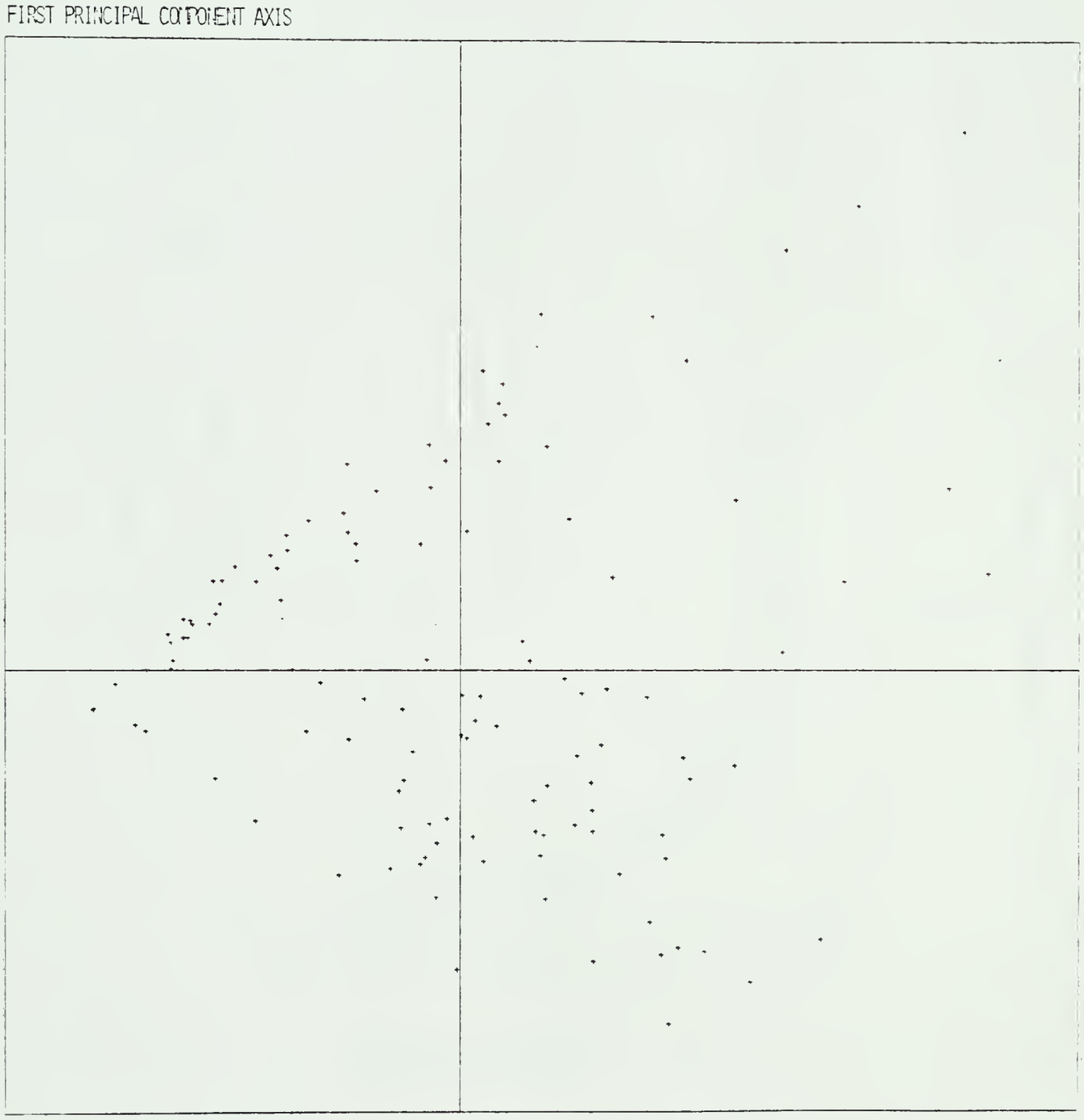

FIGURE 17. PLOT OF INDIVIDUALS FROM THE TWO PUTATIVE HYBRID STANDS, BASED ON 5 VARIABLE PRINCIPAL COMPONENT ANALYSIS.

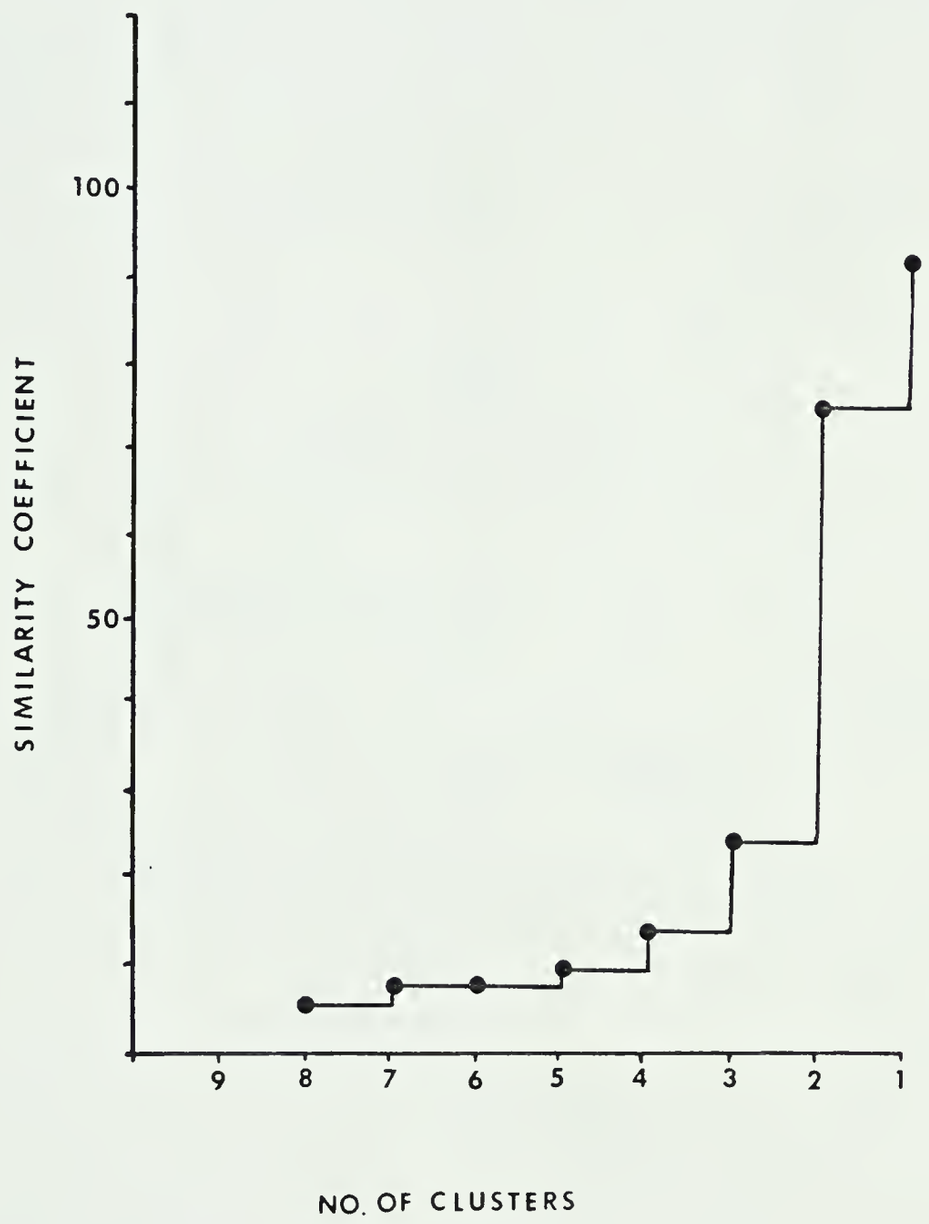

Figure 18. Similarity coefficients in 5 variable cluster analysis of the putative hybrid stands.

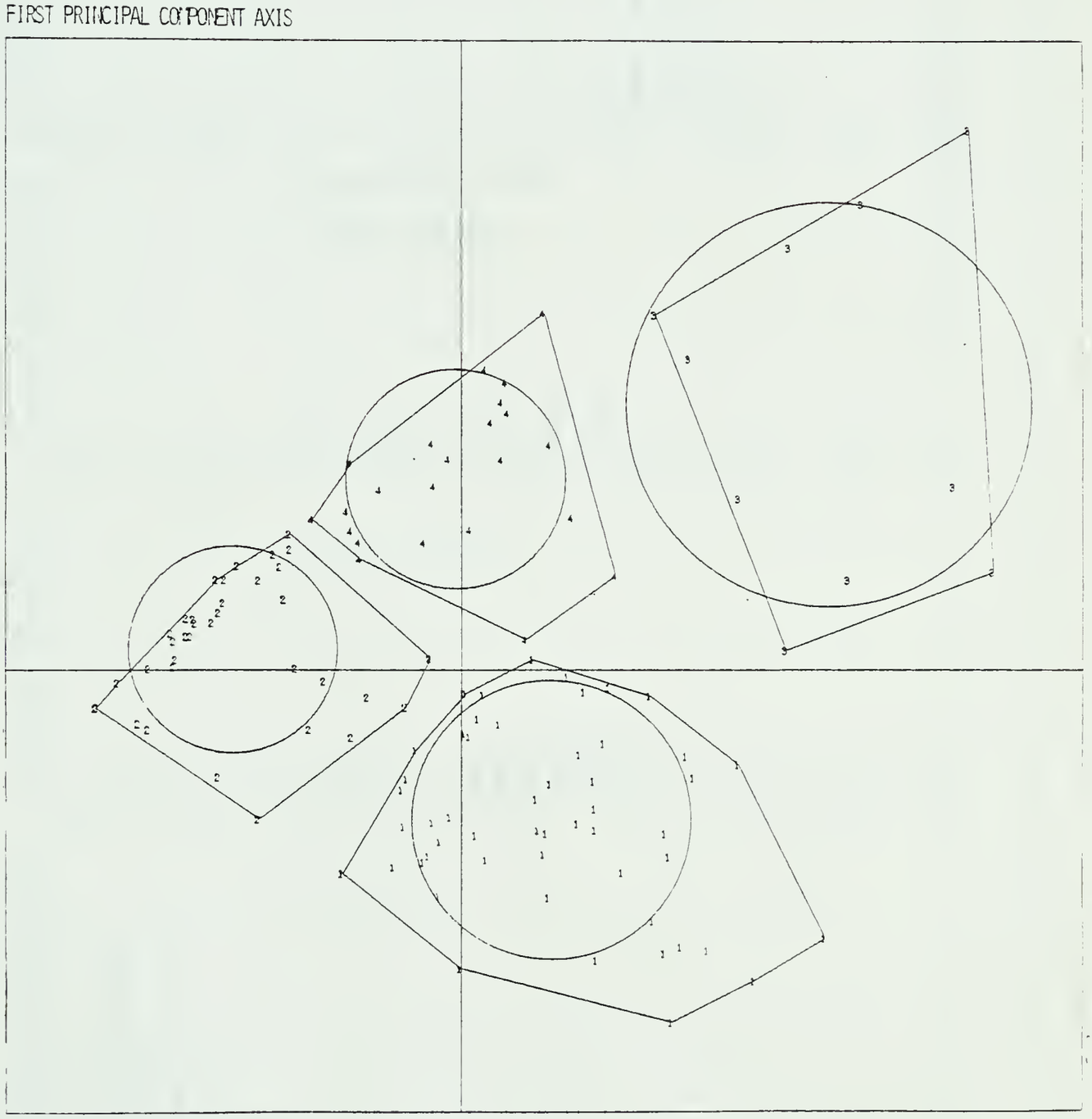

FIGURE 19. PLOT OF THE FOUR GROUPS OBTAINED FROM 5 VARIABLE CLUSTER ANALYSIS OF THE TWO PUTATIVE HYBRID STANDS.

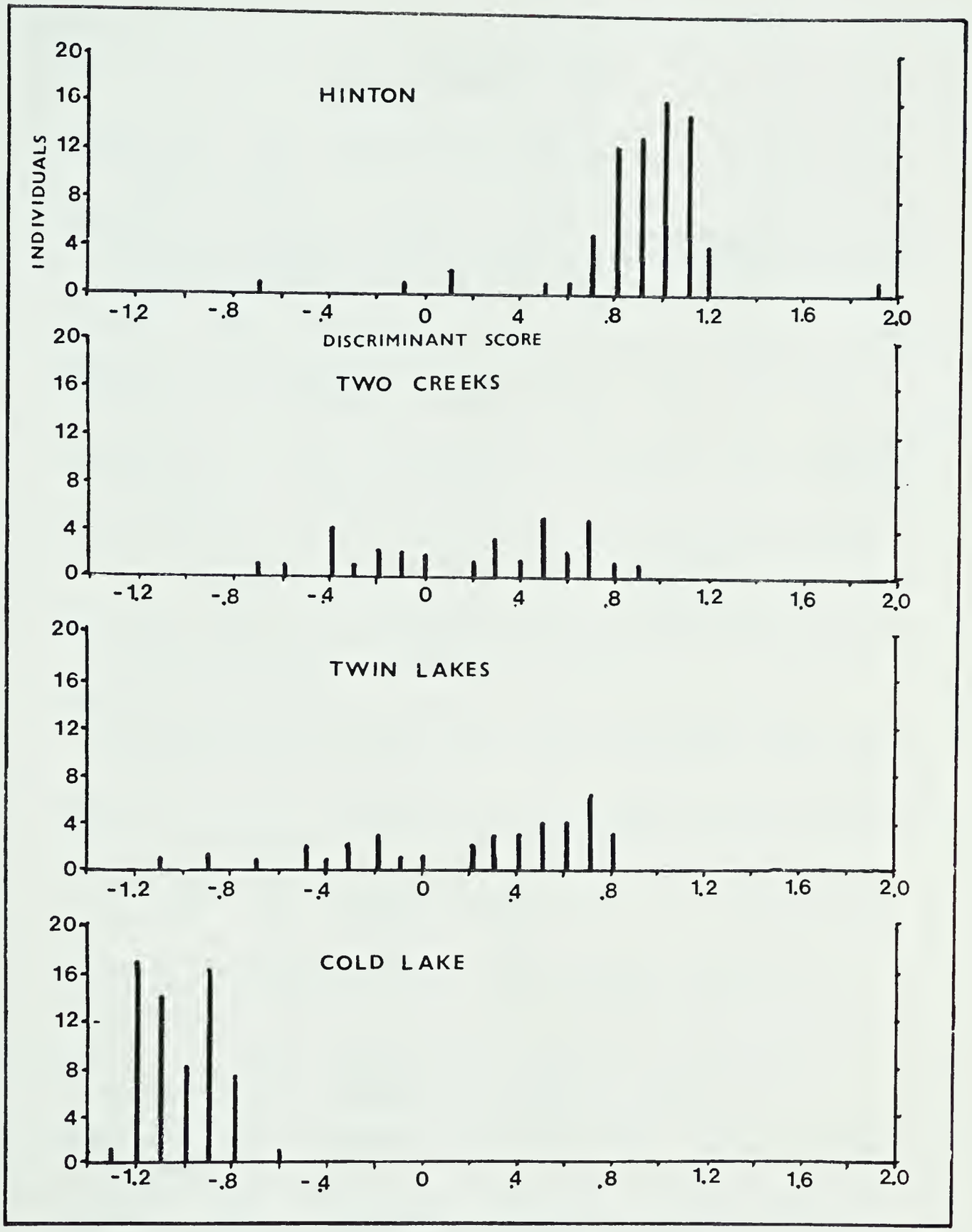

Figure 20. Discriminant scores of individuals from the Hinton, Two Creeks, Twin Lakes, and Cold Lake stands, as calculated from a four monoterpene discriminant function derived from the Hinton and Cold Lake stands.

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